

DIOPATRA AUDOUIN AND MILNE EDWARDS (POLYCHAETA: ONUPHIDAE) FROM AUSTRALIA, WITH A DISCUSSION OF DEVELOPMENTAL PATTERNS IN THE GENUS.

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ABSTRACT

This study recognizes nine Australian species of *Diopatra* Audouin and Milne Edwards, of which six are newly described. A key to adults and descriptions of all species are provided. The variability and size-dependency of two diagnostic characters (extent of the branchial region and first occurrence of subacicular hooks) are analyzed. Observations on reproduction and development are presented for eight species, including the description of larvae of one species. Analysis of all available information for the genus allows the identification of four developmental patterns ranging from brooding in the parental tube to presumed broadcast spawning.

KEYWORDS: Polychaeta, Onuphidae, *Diopatra*, Australia, size-dependent characters, developmental patterns.

INTRODUCTION

Species of the onuphid polychaete genus *Diopatra* Audouin and Milne Edwards, with their elaborately constructed tubes and exquisite, spiralled branchiae, are intriguing to the intertidal collector and therefore are well represented in museum collections. In spite of this, their taxonomy has remained confused. *Diopatra* may represent an ancient Gondwanaland genus and is best represented in warmer waters (Paxton 1986). Thus, it is surprising that only three species have been reported from Australia: *D. dentata* Kinberg, 1865 (New South Wales and Western Australia), *D. amboinensis* Audouin and Milne Edwards, 1833 (Queensland) and *D. aciculata* Knox and Cameron, 1971 (Victoria).

The present paper represents the first part of a world-wide revision of the genus and results from the study of all available material in Australian museums. The paper describes the Australian *Diopatra* fauna, discusses the variability of certain taxonomic characters, reports observations on the reproductive biology of some of the Australian species and identifies and discusses the developmental patterns in the genus.

MATERIALS AND METHODS

Complete collecting data is given only for type material examined; all other material is listed in abbreviated form. New descriptions are based on complete type series, in some cases with large size ranges; counts and measurements are those of the holotype, with the paratype ranges in parentheses. Counts and measurements in redescrptions are of the type specimen examined, with the range of other material in parentheses. Body width (without parapodia) is of setiger 10. Terminology in descriptions and procedures for SEM studies follow Paxton (1986). Scanning electron micrographs of antennae are from the proximal area where the sensory buds are flatter than those more distally. The key is artificial and is to adults only. Differential diagnoses and descriptions are given for all species.

Abbreviations used in the text are as follows: AM, Australian Museum, Sydney; MNHN, Museum National d'Histoire Naturelle, Paris; MU, Macquarie University, Sydney; NMV, Museum of Victoria, Melbourne; NRS, Naturhistoriska Riksmuseet, Stockholm; NTM, Northern Territory Museum, Darwin; QM,

Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth; ZMH, Zoologisches Institut und Zoologisches Museum, Hamburg.

SYSTEMATICS

Family Onuphidae Kinberg, 1865 Subfamily Onuphinae Kinberg, 1865

Genus *Diopatra* Audouin and Milne Edwards

Diopatra Audouin and Milne Edwards, 1833:229 (type species *Diopatra amboinensis* Audouin and Milne Edwards, 1833, by subsequent designation by Malmgren 1866:180).

Diagnosis. Tentacular cirri present; branchial filaments arranged spirally around trunk.

Remarks. For a full definition see Paxton (1986).

Key to the Australian Species of *Diopatra*

1. a Distinct dark middorsal bands on anterior setigers (Fig.31A); very long dorsal cirri (almost as long as branchiae); parapodia of setigers 5-25 with ventral lobe (Fig.31D) *D. aciculata* Knox and Cameron, 1971
- b Middorsal bands absent; dorsal cirri much shorter than branchiae; ventral lobe absent 2
2. a Styles of antennae with transverse brown pigment band 3
- b Styles of antennae without brown band 6
3. a Hooks of anterior parapodia falcate and bidentate 4
- b Hooks of anterior parapodia bidentate only 5
4. a Very small species (width of adult 2.0 mm or less); shafts of mandibles pale, calcareous cutting plates with one indentation each (Fig.24A) *D. lilliputiana* n. sp.
- b Large species (width of adult more than 3.0 mm); shafts of mandibles dark, calcareous cutting plates with two indentations each (Fig.13C) *D. maculata* n. sp.
5. a Mandibles with very dark shafts (Fig.8C) *D. dentata* Kinberg, 1865
- b Mandibles with white shafts (Fig.21C) ... *D. albimandibulata* n. sp.

6. a Calcareous cutting plates of mandibles with one indentation each (Fig.30D) *D. gigova* n. sp.
- b Calcareous cutting plates of mandibles with two indentations each (Fig.18E) 7
7. a Antennal ceratophores with brown spots; pectinate setae with 6-11 teeth (Fig.18A, B) *D. oligopectinata* n. sp.
- b Antennal ceratophores with brown rings; pectinate setae with 15-25 teeth 8
8. a Distinctive brown pigmentation on presetal lobes and bases of dorsal cirri (Fig.27B); pectinate setae flat, with thin stem (Fig.27G) *D. hanleyi* n. sp.
- b Presetal lobes and bases of dorsal cirri without pigmentation; pectinate setae often furred, with thick stem (Fig.1G, H) ... *D. amboinensis* Audouin and Milne Edwards, 1833

Diopatra amboinensis Audouin and Milne Edwards (Figs 1-6)

Diopatra amboinensis Audouin and Milne Edwards, 1833:229 (Ambon); Milne Edwards 1838:564 (check-list); Malmgren 1866:179 (designation of type species); Collin 1902:742 (Thursday Island, Queensland); Fauvel 1930:29 (indeterminable); Hartman 1959:298 (check-list); Paxton 1986:41 (generic revision).

Diopatra dentata (not Kinberg, 1865) - Augener 1922:37 (Western Australia).

Diopatra cuprea cuprea (not Bosc, 1802) - Hartmann-Schröder 1979:125, figs. 258-61 (in part) (Western Australia).

Diopatra sp. - Hartmann-Schröder 1980:63 (in part) (Western Australia).

Diopatra n. sp. 2 - Paxton 1986:21, figs. 13b, 13d, 14a, 14d (juvenile characters).

Type material. LECTOTYPE - MNHN 60a: incomplete specimen, 33 mm long (40 setigers), 4.0 mm wide, Ambon, Indonesia, 1829, coll. Quoy & Gaimard.

PARALECTOTYPE - MNHP 60b: incomplete specimen, 33 mm long (42 setigers), 5.0 mm wide, same data as lectotype.

Additional material. WESTERN AUSTRALIA - ZMH V9335: 1, Cape Jaubert; ZMHP-16651: 2, Dampier. NORTHERN TERRITORY - NTM W1773: 2, Annesley Point; NTM W2890: 1; NTM W2891: 1; NTM W2892: 1, Cape Hotham. Escape Cliffs; NTM W3899: 1; NTM W3914: 1, Darwin, creek 'H'; NTM W3087: 1; NTM W3823:

1; NTM W3873: 1; NTM W3874: 1; NTM W3875: 1; NTM W3876: 1; NTM W4207: 1; NTM W4208: 1; NTM W4209: 1; NTM W4210: 1; NTM W4211: 1, Darwin, Fannie Bay; NTM W3916: 1, Darwin Harbour; NTM W4226: 1; NTM W4227: 1; NTM W4885: 1; NTM W4886: 1; NTM W4889: 1; NTM W4972: 2, Darwin, Ludmilla Creek; NTM W3824: 1; AM W20559: 1, Darwin; NTM W539: 1; NTM W650: 3; NTM W695: 1; NTM W1524: 1; NTM W1525: 1; NTM W1526: 1; NTM W1527: 1; NTM W1531: 1; NTM W1532: 1; NTM W1533: 1, Gove; NTM W3831: 1, McArthur River, Dugong Channel; NTM W3070: 1; NTM W3072: 1; NTM W3073: 1, Port Essington, Victoria Settlement; NTM W4811: 1; NTM W5435: 1, Shell Island, East arm. QUEENSLAND - AM W20370: 4; AM W20371: 1, Abbot Point; QM G10625: 3, Bramble Bay; QM G7546: 7; AM W6036: 2; AM W6054: 2; QM GMGH563: 1; QM GMGH 564: 1; QM GMGH 5661; QM G10428: 1; QM G10453: 1, Brisbane, Moreton Bay; QM G7546: 7, Cribb Island, Serpentine Creek; AM W16504: 2, Gladstone, Auckland Creek; AM W10277: 1; AM W10281: 1; AM W10282: 1; AM W13325: 18; AM W13326: 1; AM W13327: 1; AM W16427: 2; AM W199385: 100+, Gladstone, Calliope River; QM G10555: 1, Gladstone Harbour; QM G10691: 7, Gladstone, Haye Point; AM W198986: 6, Halifax Bay; AM W20560: 2, Townsville.

Complete specimens range from a juvenile 14 mm long (80 setigers) and 1.2 mm wide, to an ovigerous female of length 170 mm (320 setigers) and width 5.0 mm. Incomplete specimens range in width from 0.5 to 6.0 mm.

Diagnosis. Antennal styles with brown specks; four pairs of modified parapodia with bidentate pseudocompound hooks with short appendages; 10-20 transverse, often rolled up pectinate setae with 15-20 teeth at setiger 40; limbate setae with proximal shelves; mandibles with black shafts and calcareous cutting plates with two indentations each; maxilla 1 with medially extended falcate arch.

Description. Types and many specimens without colour pattern, others with varying amounts of brown pigmentation. Prostomium, palps and antennal styles usually with diffuse specks, antennal ceratophores with brown rings, peristomium and anterior 10-15 setigers uniformly brown or with diffuse bands.

Prostomium (Fig. 1A) anteriorly short and rounded with subulate frontal palps. Ceratophores of antennae with 11-13 (9-15) proximal rings and a longer distal ring. Styles relatively long, taper-

ing distally, posterior antennae about equal in length to setiger 9-12 (13-22), anterior laterals to 4-5 (4-11). Styles with 16-18 interrupted longitudinal rows of sensory buds (Fig. 2A). Buds slightly raised; pores of serous glands forming complete circles (Fig. 2B). Nuchal grooves forming 3/4 circles. Tentacular cirri very long, about 2.5 to 3 times as long as peristomium, tapering distally, inserted subdistally on moderately long peristomium, almost lateral to posterior lateral antennae.

Anterior parapodia with rounded presetal and subulate postsetal lobes (Fig. 1B). Presetal lobe present to setiger 10-15, postsetal lobe becoming gradually smaller, but remaining as a small boss at end of body. Dorsal cirri subulate, becoming more slender posteriorly; ventral cirri subulate on anterior 4 (4-5) setigers. Spiralled branchiae (Fig. 1C) from setiger 5 (4-5), best developed on setigers 6-12, with 11 (up to 12) whorls, reaching to anterior part of prostomium when extended anteriorly. Individual filaments long and slender. Number of filaments decreasing gradually after setiger 12, single filaments from setiger 24-71 depending on size (Fig. 3), absent shortly thereafter.

Modified parapodia (setigers 1-4) with 1-2 slender upper limbate setae and bidentate pseudocompound hooks with short appendages and short pointed hoods. Each parapodium with 1 large median (Fig. 1D) and 2-3 less robust hooks (Fig. 1E) projecting from main setal pocket, and 1-2 slender hooks (Fig. 1F) from small lower pocket.

Unmodified parapodia (setiger 5 onwards) with pectinate and limbate setae. Pectinate setae with 15-20 long teeth in transverse combs, edges often partly rolled inwards (Fig. 1G, 1H); about 10-20 pectinate setae present per parapodium at setiger 40. Limbate setae (Fig. 1I, 1J) with wide, strongly serrated proximal shelves and slender wings. Lower limbate setae replaced by 2 bidentate subacicular hooks from setiger 19-20 (11-23), depending on size of worm (Fig. 4).

Pygidium with two pairs of short anal cirri; dorsal pair as long as last four setigers, ventral pair 3/4 thereof.

Mandibles (Fig. 5A) with slender slightly diverging shafts. Distal two-thirds of shafts darkly sclerotized, lateral shelves and proximal parts pale. Calcareous cutting plates high, having two distal indentations each. Maxillae moderately sclerotized; Mx 1 characterized by medially extended falcate arch (Fig. 5B, C). Some specimens with symmetrical maxillae, i.e. either lacking

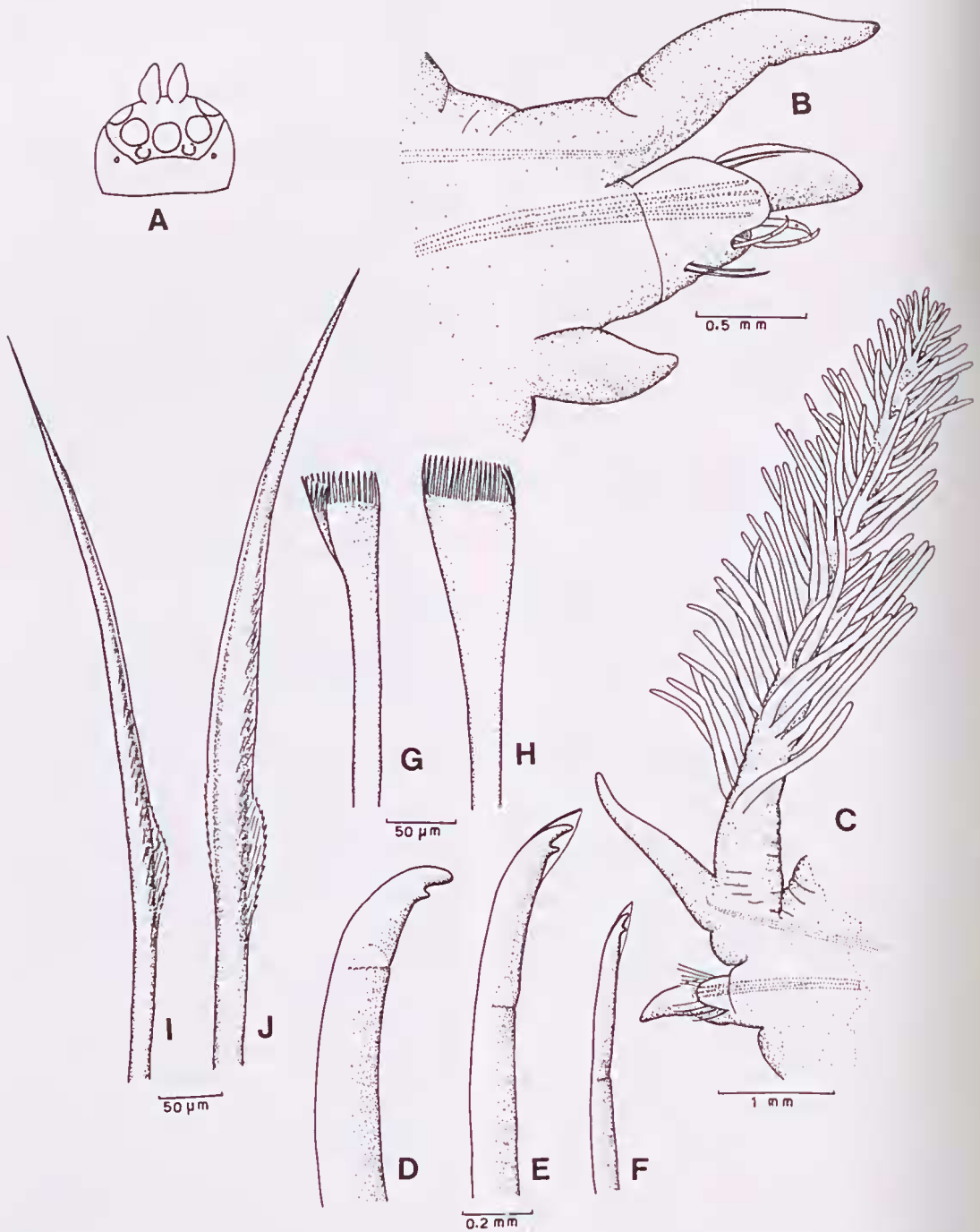


Fig. 1. *Diopatra amboinensis*: (B-G: paralectotype, MNHN 60b; H-J: NTM W4972). A, stylized diagram of prostomium and peristomium, dorsal view; B, parapodium 1, anterior view; C, parapodium 6, same view; D, large median pseudocompound hook from setiger 2; E, less robust pseudocompound hook from same; F, slender pseudocompound hook from same; G, rolled up pectinate seta from setiger 38; H, almost flat pectinate seta from setiger 40; I, upper limbate seta from setiger 40; J, median limbate seta from same.

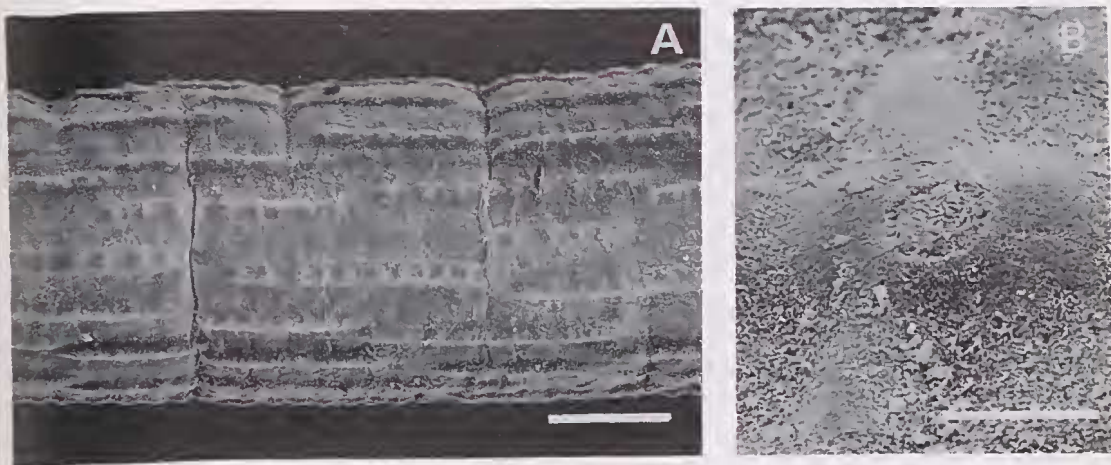


Fig. 2. Scanning electron micrographs of antenna of *Diopatra amboinensis*: A, rows of sensory buds (scale 100 µm); B, enlarged sensory bud (scale 10 µm).

Mx III completely, or both left and right pieces present. Maxillary formula (based on 10 specimens): Mx I = 1 + 1; Mx II = 6 (4-8) + 8 (5-8); Mx III = 6 (0-9) + 0 (0-7); Mx IV = 5 (5-9) + 7 (5-11); Mx V = 1 + 1.

Tubes consisting of soft inner layer with outer layer of muddy sand predominantly with pieces of vegetation and occasional shells attached in close circles.

Remarks. The type material consists of two specimens (MNHN 60a and 60b). Both specimens are in relatively good condition, with 60a

being the better one. They are accompanied by printed labels, dated 1868, presumably the time of museum registration and another handwritten label, dated 1829, presumably the date of collection. The printed label of specimen 60a has a red border, while 60b does not. Although Audouin and Milne Edwards did not designate a holotype, they, or a museum curator, may have intended the specimen with the red bordered label as such. Therefore, I am hereby designating specimen MNHN 60a the lectotype and MNHN 60b the paralectotype.

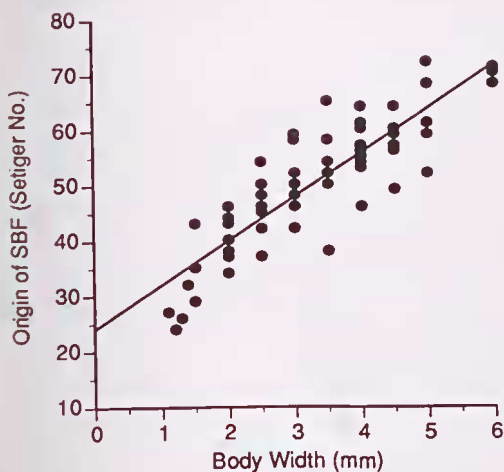


Fig. 3 *Diopatra amboinensis*: Relationship between body width of specimens and origin of single branchial filaments (SBF); [$r^2 = 0.746$, $y = 7.9x + 24$, $P < 0.0001$ (significance of overall regression)].

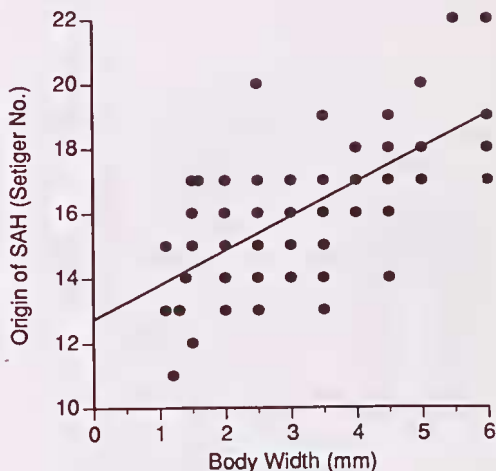


Fig. 4. *Diopatra amboinensis*: Relationship between body width of specimens and origin of subacicular hooks (SAH) [$r^2 = 0.414$, $y = 1.1x + 12.7$, $P < 0.0001$ (significance of overall regression)].

Diopatra amboinensis was described from Ambon, Indonesia. The original description was vague by modern standards; the species was considered indeterminable (Fauvel 1930) and remained rarely reported. Reports by Willey (1905), Pflugfelder (1929) and Lieber (1931) referred to other species, the identities of which are still unclear. Examination of the type material confirms that a widely distributed Australian species is indeed *D. amboinensis*.

Diopatra amboinensis is a "generalized species", lacking any striking characteristics, and therefore at times is difficult to distinguish from other species. It can generally be identified by the following combination of characters: antennal ceratophores with brown rings, antennal styles without a brown band, long and slender antennae and tentacular cirri, late occurrence of subacicular hooks, mandibles with dark shafts and calcareous plates with two distal indentations. If these characters cannot be utilized as a result of loss of pigment, dissolution of calcareous plates, etc., then maxilla I should be examined. In medium to large specimens the falcate arch is extended medially into a flattened shelf (Fig. 5B, C). Among the species sympatric with *D. amboinensis* this character is present only in *D. hanleyi*. However, these two species can be distinguished easily by their different setae.

Augener (1922:37) reported *D. dentata* from Cape Jaubert, Western Australia. The specimen (ZMH V9335) has been examined and, despite its poor condition, was re-identified as *D. amboinensis* because of its brown ceratophoral

rings, relatively long tentacular cirri and late occurrence of subacicular hooks.

Biology. Specimens collected from March to August contain gametes in their body cavities. The largest ova measure 200-230 μm in diameter. Although some specimens indicate recent spawning, no eggs or developing young were found in any tubes or attached to them.

Distribution. Ambon, Indonesia; Western Australia, Northern Territory, Queensland, Australia (Fig. 6); intertidal to 25 m.

Diopatra dentata Kinberg
(Figs 6, 7-11)

Diopatra dentata Kinberg, 1865:560; 1910:39, pl. 13, fig. 5 (Sydney, 22 m); Augener 1922:27 (examination of types); Pope 1943: 247 (Sydney); Hartman 1948:86 (examination of types); Dakin *et al.* 1952:149, pl. 29 fig. 5, text-fig. 16 (New South Wales); Bennett 1966:79, pl. 54 (New South Wales); Day and Hutchings 1979:118 (check-list); Hutchings and Murray 1984:45 (New South Wales); Paxton 1986:38 (New South Wales); Hartmann-Schröder 1990:65 (in part) (Maclean, New South Wales).

Diopatra, sp. - Hartmann-Schröder 1989:39 (Eden, New South Wales).

Type material. SYNTYPES - NRS T- 460: 2 posteriorly regenerated juveniles in poor condition. Excluding the regeneration, they measure 18 mm long (40 setigers), 2.5 mm wide and 16 mm long (41 setigers), 2.0 mm wide, respectively. The material also includes 2 median

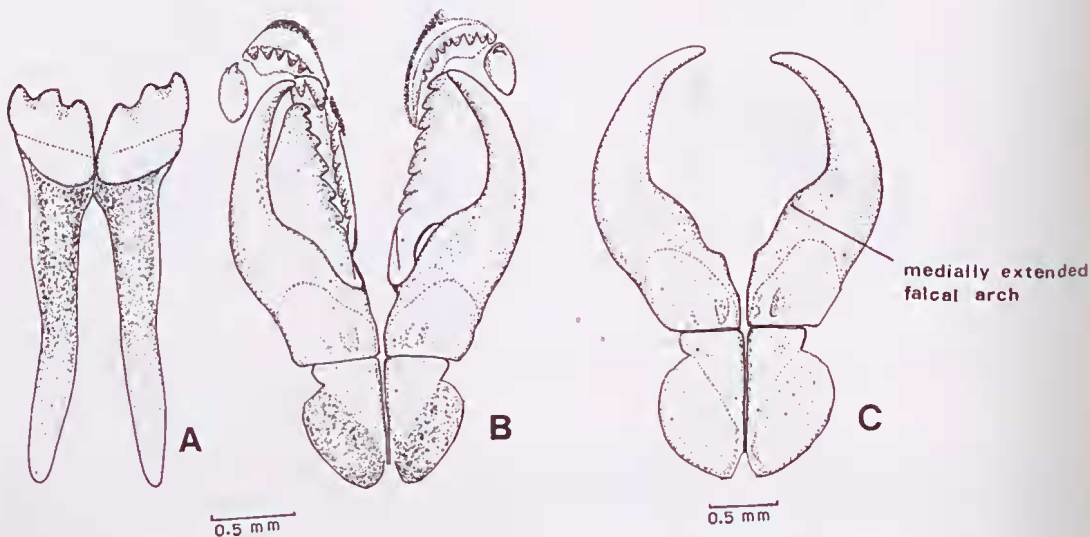


Fig. 5. *Diopatra amboinensis*: (A-B: NTM W3824; C: paralectotype, MNHP 60b). A, mandibles; B, maxillae; C, carriers and maxillae I.

fragments of a larger diameter and a squashed head. Sydney, New South Wales, Eugenie Expedition, 22 m.

Additional material. NEW SOUTH WALES
- AM W20364 : 12, Arrawarra; AM W20361: 1, Batemans Bay; AM W20365: 3, Crowdy Head; ZMH P-19777: 1, Eden, Quarantine Bay; AM W200191: 3; AM W200192: 6; AM W200193: 3; AM W200194: 4; AM W200195: 1; AM W200196: 2; AMW200197: 2; AMW200199: 2; AMW200200: 2; AM W200201: 1; AM W200202: 1, Eden, Two-fold Bay; AM W198484: 1; AM W198494: 1, Gerroa, Black Head; AMW1750: 2; AMW197931: 3, Gunnamatta Bay; AM W196434: 1; AM W196435: 2; AM W196436: 1; AM W20397: 6; AM W20402: 2; AM W20403: 6, Hawkesbury River; AM W17466: 1; AM W194249: 4; AM W194374: 1; AM W194412: 2; AM W194432: 7; AM W194450: 4; AM W194575: 1; AM W194379: 5; AM W20396: 1; AM W20398: 1; AM W20399: 1, Jervis Bay; ZMH P-19704: 13, Maclean; AM

W198984: 4, Minnie Water; AM W20360: 1, Port Kembla; AM W20362: 1, Port Stephens; AM W9644: 3; AM W9665: 1; AM W9683: 2; AM W9707: 4; AM W9805: 1; AM W9810: 3; AM W9832: 1; AM W9854: 2; AM W9883: 1; AM W9904: 3; AM W9944: 2; AM W10002: 1; AM W10050: 2; AM W10926: 1; AM W10975: 1; AM W10989: 2; AM W18849: 7; AM W18903: 2; AM W18964: 4; AM W19027: 1; AM W194215: 4; AM W195460: 4; AM W195527: 1; AM W195661: 3; AMW195697: 3; AMW195772: 1, Sydney, Botany Bay; AM W20359: 11, Sydney, Bottle and Glass Rocks; AM W20401: 7, Sydney, Chinaman's Beach; AM W20567: 2, Sydney, Cronulla Beach; AM W17679: 1; AM W17690: 3, Sydney, Kurnell; AM W20391: 1, Sydney, Little Manly Cove; AM W3771: 1; AM W3826: 1; AM W4418: 1; AM W4757: 2; AM W20363: 7; AM W20566: 2, Sydney, Long Reef; AM W20400: 2, Sydney, Manly; AM W20395: 6, Sydney, Middle Harbour; AM W20394: 6; AM W20392: 9; AM W20393: 5,

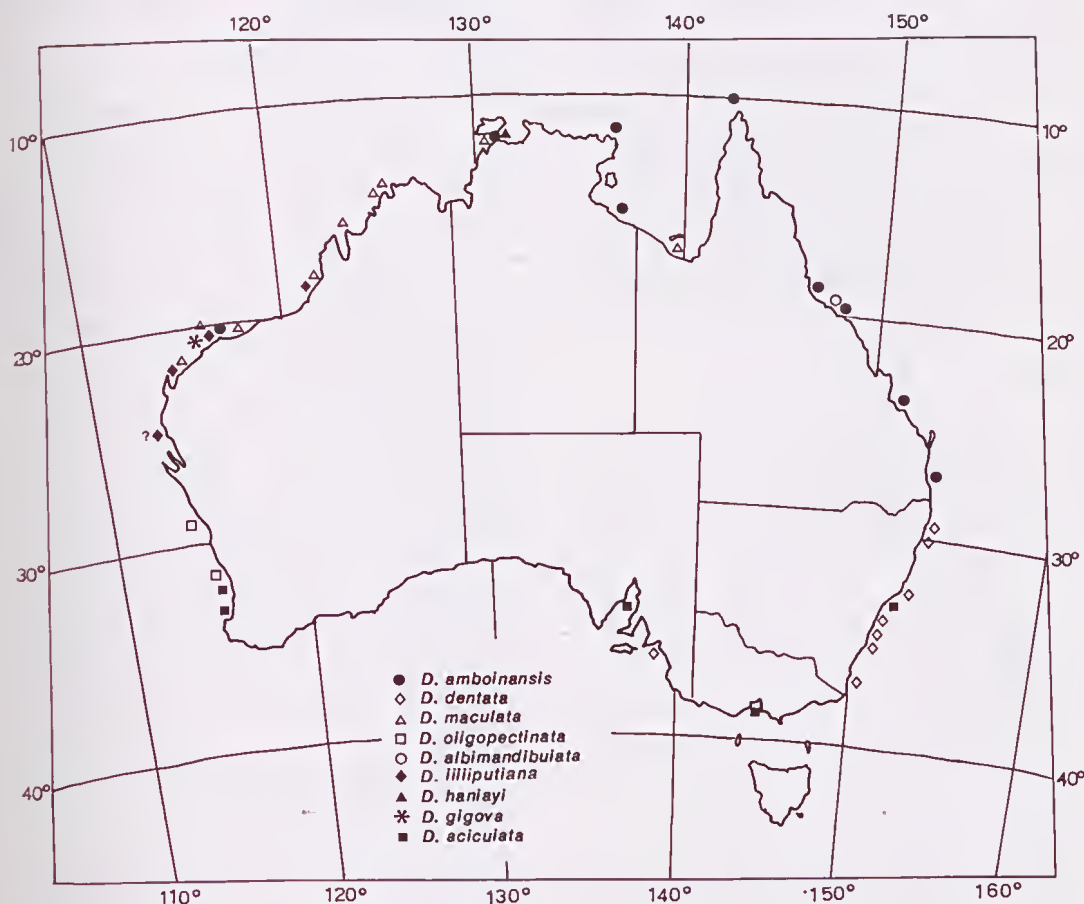


Fig. 6. Distribution of Australian species of *Diopatra*.

Sydney, Nielsen Park; AM W20366: 6, Sydney, Watson's Bay; AM W6912: 1; AM W6913: 6, Sydney; AM W3292: 3, Yamba, Green Point; SOUTH AUSTRALIA - AM W20565: 1, Murray River Heads.

Complete specimens range from 12 mm in length (62 setigers) and 1.0 mm in width to 245 mm in length (355 setigers) and 6.0 mm in width. Greatest width of incomplete specimens 7.0 mm.

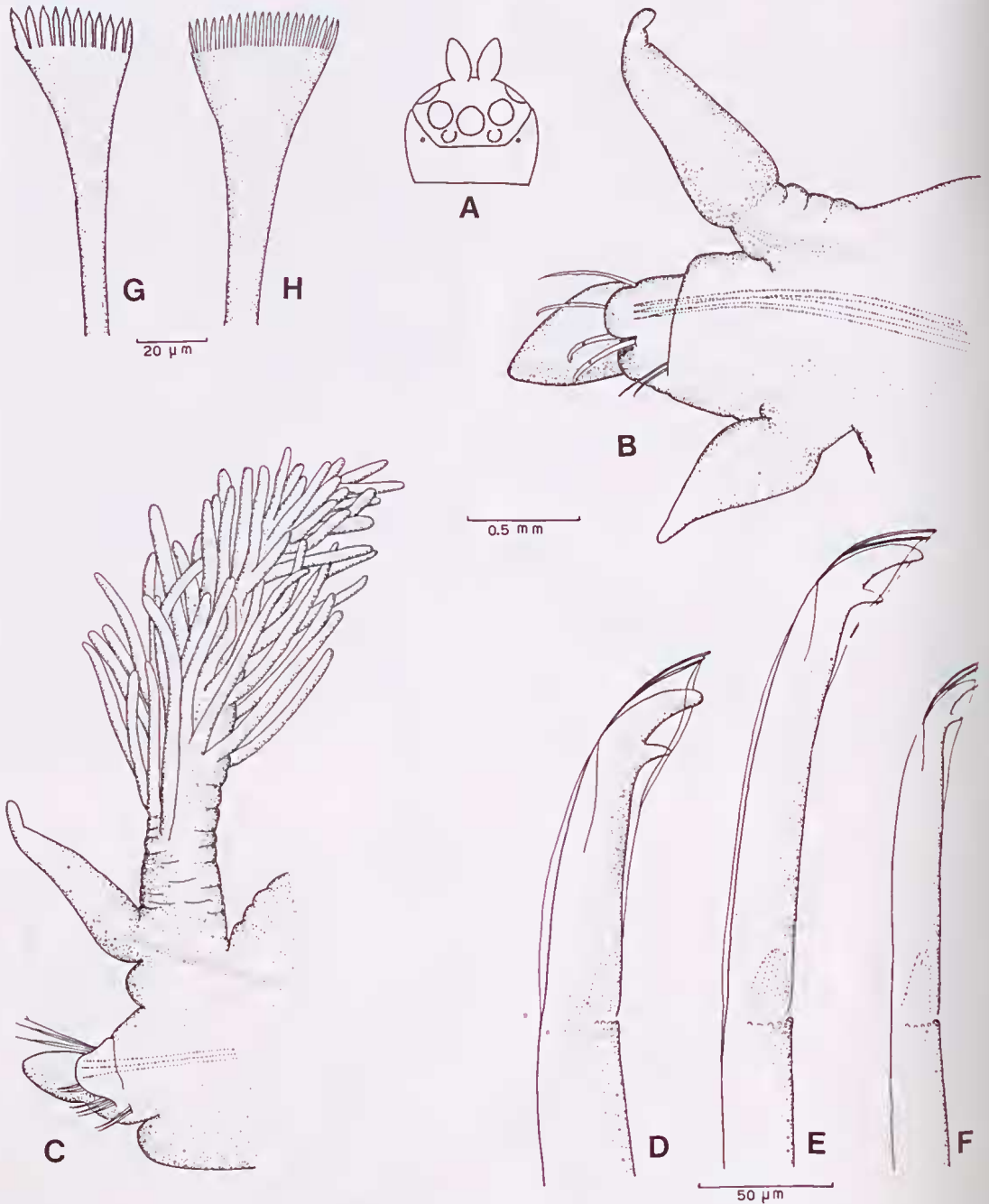


Fig. 7. *Diopatra dentata*: (B-G: AM W20394; H: AM W20393). A, stylized diagram of prostomium and peristomium, dorsal view; B, parapodium 1, anterior view; C, parapodium 6, same view; D, large median pseudocompound hook from setiger 1; E, less robust pseudocompound hook from same; F, slender pseudocompound hook from same; G, pectinate seta with 11 teeth from setiger 40; H, same with 20 teeth from setiger 39.

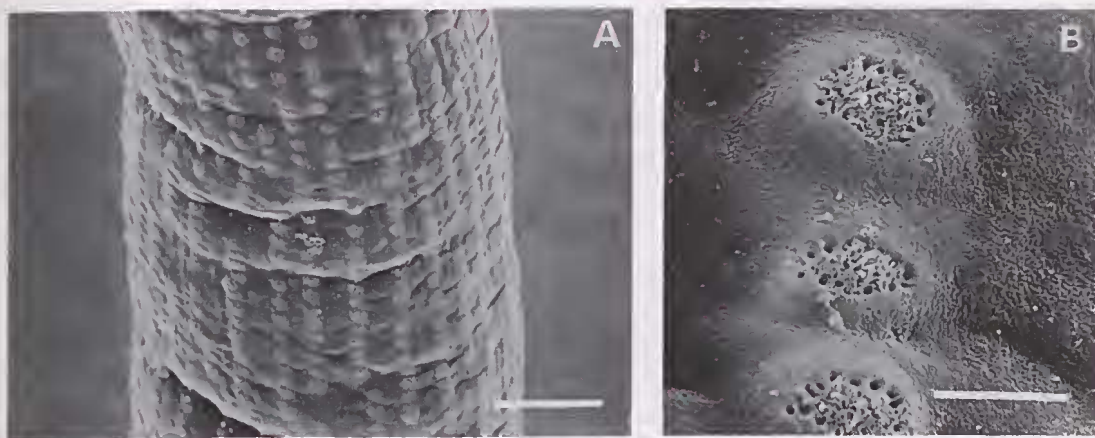


Fig. 8. Scanning electron micrographs of antenna of *Diopatra dentata*: A, rows of sensory buds (scale 100 µm); B, enlarged sensory buds (scale 10 µm).

Diagnosis. Antennal styles with median brown band; four pairs of modified parapodia with bidentate pseudocompound hooks with short to long appendages; 5-15 transverse pectinate setae with 11-20 teeth each at setiger 40; limbate setae with proximal shelves; mandibles of mature specimens with black shafts and calcareous cutting plates with one indentation each.

Description. Colour markings consisting of brown specks to overall light brown on prostomium and anterior setigers (faded in alcohol). Styles of antennae with median transverse brown bands.

Prostomium (Fig. 7A) anteriorly rounded, with pair of subulate frontal palps. Ceratophores of antennae with 10-11 (9-13) proximal rings and a longer distal ring. Styles short to moderately long, tapering only slightly towards distal end, with blunt to bulbous tips; posterior antennae about equal to setiger 7-10 (7-16, most often 10-12), anterior laterals to 2-5 (3-9). Styles with 24-26 interrupted longitudinal rows of sensory buds (Fig. 8A); buds slightly raised, pores of serous glands forming complete circles (Fig. 8B). Nuchal grooves 3/4 circles. Tentacular cirri stout, moderately long, about 2(1-2) times as long as peristomium; inserted subdistally on moderately long peristomium, almost lateral to posterior lateral antennae.

Anterior parapodia with rounded presetal and thick subulate postsetal lobes (Fig. 7B). Presetal lobe present to setiger 6-8; postsetal lobe becoming gradually smaller, but remaining as distinct lobe at end of body. Dorsal cirri subulate, becoming more slender posteriorly; ventral cirri subulate on anterior 4 setigers. Spiralled branchiae (Fig.

7C) from setiger 5 (4-5), best developed on setigers 6-9, with up to 10 whorls, reaching to peristomium when extended anteriorly. Individual filaments moderately long and slender. Number of filaments decreasing gradually after setiger 9, single filaments from setiger 28-62, depending on size (Fig. 9), absent shortly thereafter.

Modified parapodia (setigers 1-4) with 1-2 slender upper limbate setae and bidentate hooks. Each parapodium with 1-2 large median (Fig. 7D) and 2-3 less robust hooks (Fig. 7E) projecting from main setal pocket, and 2 slender hooks (Fig. 7F) from small lower pocket. Large hooks

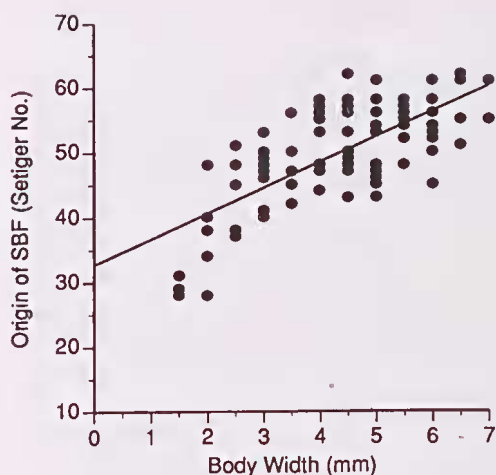


Fig. 9. *Diopatra dentata*: Relationship between body width of specimens and origin of single branchial filaments (SBF) [$r^2 = 0.500$, $y = 3.9x + 32.7$, $P < 0.0001$ (significance of overall regression)].

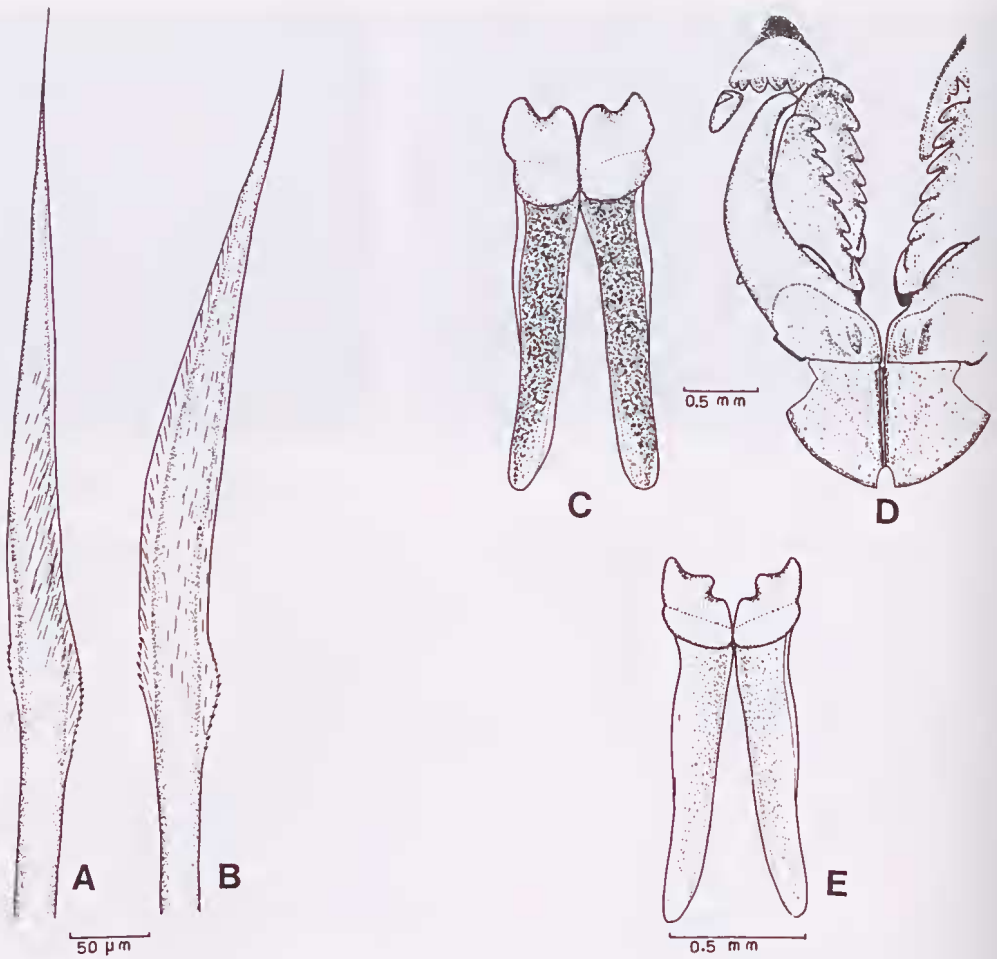


Fig. 10. *Diopatra dentata*: (A-B: AM W20393; C-D: AM W20394; E: AM W20400). A, upper limbate seta from setiger 39; B, median limbate seta from same; C, mandibles of large specimen; D, maxillae of same; E, mandibles of juvenile.

almost simple, others pseudocompound with short to long appendages; with short hoods.

Unmodified parapodia (setiger 5 onwards) with pectinate and limbate setae. Pectinate setae (Fig. 7G, H) from setiger 5-6 with 11-20 teeth in transverse combs; 5-15 (most often 10-15) pectinate setae per parapodium at setiger 40. Limbate setae (Fig. 10A, B) with wide, strongly serrated proximal shelves and wide wings. Lower limbate setae replaced by 2 bidentate subacicular hooks from setiger 13-14 (11-18, most often 13-15), not markedly size-dependent (Fig. 11).

Pygidium with two pairs of anal cirri; dorsal pair about as long as 10 last segments, ventral pair half as long.

Mandibles strongly sclerotized, black in large specimens, except for thin lateral shelves; calcareous cutting plates high, with one median

distal indentation each. In large specimens plates almost square and touching medially (Fig. 10C), in smaller specimens more flared and with 2 distal indentations (Fig. 10E). Maxillae (Fig. 10D) also very darkly sclerotized, in large worms almost black. High incidence of symmetrical maxillae; Mx III may be present on right and left side or totally absent. Maxillary formula (based on 10 specimens): Mx I = 1 + 1; Mx II = 8 (5-7) + 8 (5-8); Mx III = 8 (0-8) + 0 (0-8); Mx IV = 6 (4-7) + 8 (5-8); Mx V = 1 + 1.

Tubes with tough, parchment-like inner layer and outer layer of predominantly shell fragments with other foreign particles attached at right angle in close circles.

Remarks. *Diopatra dentata* is a difficult species to define. While certain diagnostic characters (e.g. relatively short antennae with median

dark band and bulbous tips, pseudocompound hooks with long appendages, mandible with single distal incision) are clearly recognizable in most individuals, they vary slightly in others and with size. The best diagnostic character is the almost square cutting plate of the mandible with its single distal indentation (Fig. 10C). However, in animals of less than 4 mm width this characteristic is not yet clearly developed. In very young individuals (up to 2.5 mm width) the cutting plates have two distal incisions (Fig. 10E), the inner of which is deeper and more pronounced. With increasing size this incision moves to a median position in the plate and the outer is lost.

Specimens from the Hawkesbury River, Sydney, differ consistently in having a smaller number of pectinate setae, limbate setae with less pronounced proximal shelves, longer antennae and softer inner linings to their tubes. They have been included here tentatively until a future electrophoretic study can clarify whether they are really conspecific.

Augener reported *D. dentata* from Western Australia. The specimen from Cape Jaubert (1922:37) has been examined in the present study and is referred to *D. amboinensis* (see remarks under *D. amboinensis*). The specimen reported as "*Diopatra* sp. (?*dentata*)" from Shark Bay (1922:281) is either a juvenile of uncertain identity or *D. lilliputiana* n. sp. (see remarks under *D. lilliputiana* n. sp.).

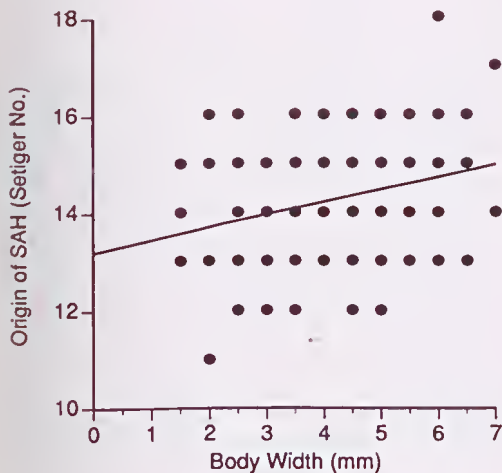


Fig. 11. *Diopatra dentata*: Relationship between body width of specimens and origin of subacicular hooks (SAH) [$r^2 = 0.073$, $y = 0.59x + 13.2$, $P = 0.0323$ (significance of overall regression)].

Hartmann-Schröder (1990: 65) reported *D. dentata* from Maclean, New South Wales and Brisbane, Queensland, stating that the species was identified by me. I have only seen the specimens from Maclean and consider Hartmann-Schröder's first record of *D. dentata* from Queensland as doubtful.

Biology. Specimens collected from October to February were distended with eggs (measuring 240-260 μ m in diameter) or mature sperm. No eggs or developing young were found in any tubes or attached to them.

Distribution. New South Wales and Murray River Heads, South Australia (Fig. 6); intertidal to 30 m.

Diopatra maculata sp. nov.
(Figs 6, 12-16)

Diopatra cuprea cuprea (not Bosc, 1802) - Hartmann-Schröder 1979:125, figs. 258-61 (in part) (Western Australia).

Diopatra sp. - Hartmann-Schröder 1980:63 (in part) (Western Australia).

Type material. HOLOTYPE - AM W19748: incomplete specimen, ovigerous, 47 mm long (104 setigers), 5.0 mm wide, Shirley Island, Western Australia, 16°17'S, 123°26'E, mangrove to sand, reef, 26 July 1988 coll. P. Hutchings sta. 115. 7

PARATYPES - AM W19746: 1 posteriorly regenerated complete specimen, 170 mm long (240 setigers), 4.5 mm wide, 1 incomplete specimen 42 mm long (49 setigers), 6.5 mm wide. Western Australia, Corneille Island, 14°12'S, 125°44'E, intertidal, 19 July 1988 coll. P. Hutchings sta. 65. AM W19688: 1 posteriorly regenerated complete specimen, with tube and attached larvae, 100 mm long (155 setigers), 7.0 mm wide. Western Australia, Enderby Island, Dampier Archipelago, 20°36'S, 116°30'E, northern beach, 29 March 1987 coll. P. Hutchings. AM W20369: 1 incomplete specimen, with 7 empty tubes, 85 mm long (127 setigers), 5.5 mm wide. Western Australia, Finucane Island, Port Hedland, in pool on reef at low tide, 21 June 1970 coll. E. Pope. ZMH P16650: 2 incomplete specimens, with 1 tube, 52-87 mm long (73-117 setigers), 5.5-6.0 mm wide. Western Australia, Onslow, Beadon Creek, slope in front of mangrove, 7 October 1975 coll. G. Hartmann-Schröder. NTM W4808: 1 complete specimen in 2 parts, together 75 mm long (163 setigers), 3.0 mm wide. Northern Territory, Shell Island, East

arm, rocky intertidal, 18 March 1988 coll. A. Mussig sta. RH88-37.

Additional material. WESTERN AUSTRALIA - NTM W4588: 1, Broome, front

Roebuck Bay; NTM W2301: 1, Broome, main wharf; NTM W2132: 1, Broome, Mangrove Point; AM W194002: 4; AM W194003: 1, Mermaid Sound; ZMH: 4, Port Hedland; AM

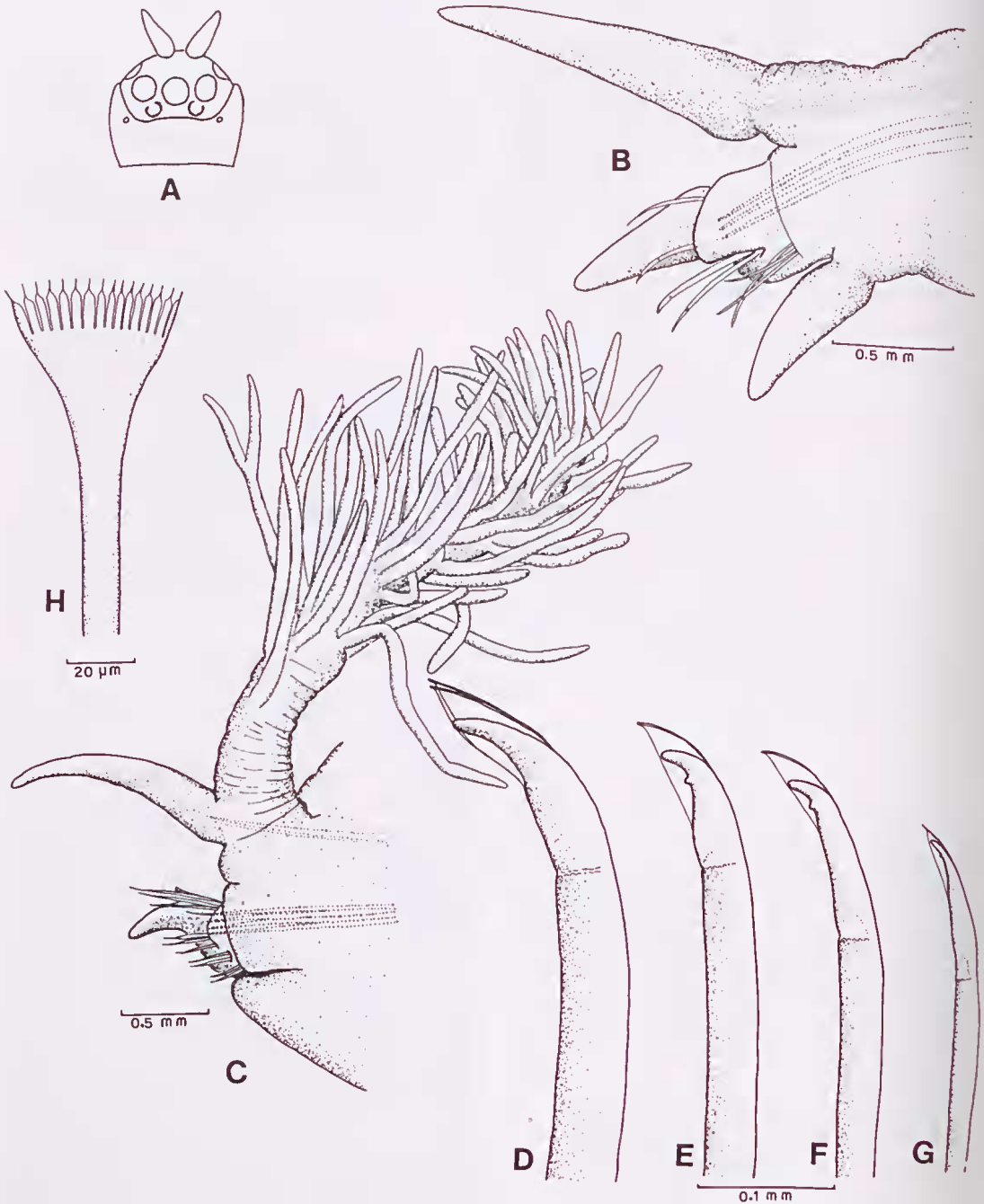


Fig. 12. *Diopatra maculata* sp. nov.: (B- C, E-H: holotype AM W19748; D: paratype AM W19688). A, stylized diagram of prostomium and peristomium, dorsal view; B, parapodium 1, anterior view; C, parapodium 7, same view; D, large median falcate pseudocompound hook from setiger 1; E, large median weakly bidentate pseudocompound hook from same; F, less robust weakly bidentate pseudocompound hook from same; G, slender weakly bidentate pseudocompound hook from same; H, pectinate seta from setiger 40.

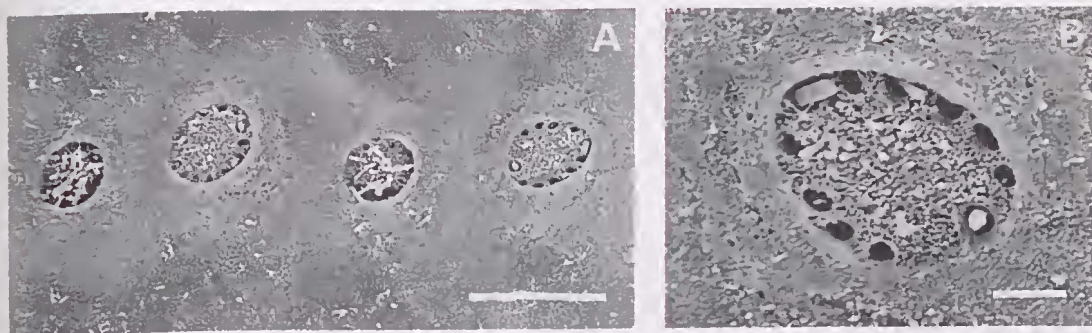


Fig. 13. Scanning electron micrographs of antenna of *Diopatra maculata* sp. nov.: A, row of sensory buds (scale 10 µm); B, enlarged sensory bud (scale 2 µm).

W19747: 1, Prudhoe Island, beach and rock platform. NORTHERN TERRITORY - NTM W3805: 1; NTM W3912: 1; NTM W3915: 1; NTM W3918: 1, Darwin, creek 'H'. QUEENSLAND - AM W6864: 1, S of Sweers Island, 10-12 m.

Specimens range from a complete juvenile 14 mm long (63 setigers) and 0.8 mm wide to a posteriorly regenerated adult 170 mm long (240 setigers) and 4.5 mm wide. The greatest width of incomplete specimens is 9.0 mm.

Diagnosis. Antennal styles with median brown band; four pairs of modified parapodia with falcate to weakly bidentate pseudocompound hooks; limbate setae with proximal shelves.

Description. Colour pattern (partly or completely faded in some specimens) consisting of irregular brown spots on prostomium, palps, ceratophores and anterior setigers; median part of styles with wide transverse brown band.

Prostomium (Fig. 12A) anteriorly short and rounded with subulate frontal palps slightly separated from each other. Ceratophores of antennae with 10-12(10-13) proximal rings and a longer distal ring, styles moderately long, tapering towards distal end. Posterior antennae about equal in length to setiger 14-16(12-18), anterior laterals to 8-9(6-9). Styles with 16-18 interrupted longitudinal rows of sensory buds (Fig. 13A). Buds flat, circles clearly demarcated, pores of serous glands irregularly spaced (Fig. 13B). Nuchal grooves forming 3/4 circles. Tentacular cirri moderately long, about 1.5 times length of peristomium (or equal to ceratophores); inserted subdistally on long peristomium, almost lateral to posterior lateral antennae.

Anterior parapodia with truncated presetal lobe and subulate postsetal lobe (Fig. 12B). Presetal lobe present to setiger 5-6, postsetal lobe becoming gradually smaller, but remaining

as small boss to near end of body. Dorsal cirri long, subulate, becoming more slender posteriorly; ventral cirri subulate on anterior 4 (4-5) setigers. Spiralled branchiae (Fig. 12C) from setiger 5, best developed on setigers 7-15, with 5 (5-10) whorls, reaching to peristomium when extended anteriorly. Individual filaments long and slender. Number of filaments decreasing gradually after setiger 15, single filaments from setiger 58(54-68), absent shortly thereafter (see Fig. 14 for range of all specimens examined).

Modified parapodia (setigers 1-4) with 1-2 slender upper limbate setae and falcate to weakly bidentate hooks. Each parapodium with 1 large median (Fig. 12D, E) and 2-3 less robust hooks (Fig. 12F) projecting from main setal pocket, and 2-3 slender hooks (Fig. 12G) from small lower

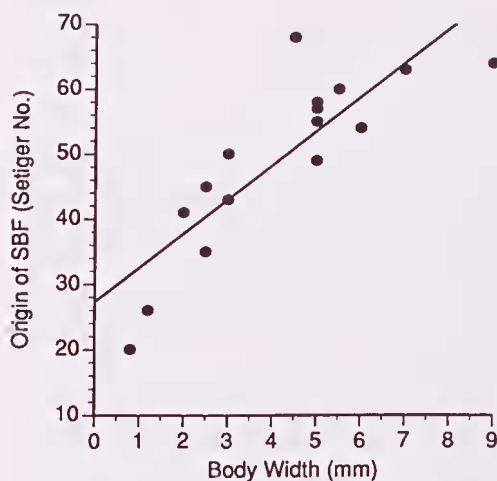


Fig. 14. *Diopatra maculata* sp. nov.: Relationship between body width of specimens and origin of single branchial filaments (SBF) [$r^2 = 0.713$, $y = 5.2x + 27.3$, $P < 0.0001$ (significance of overall regression)].

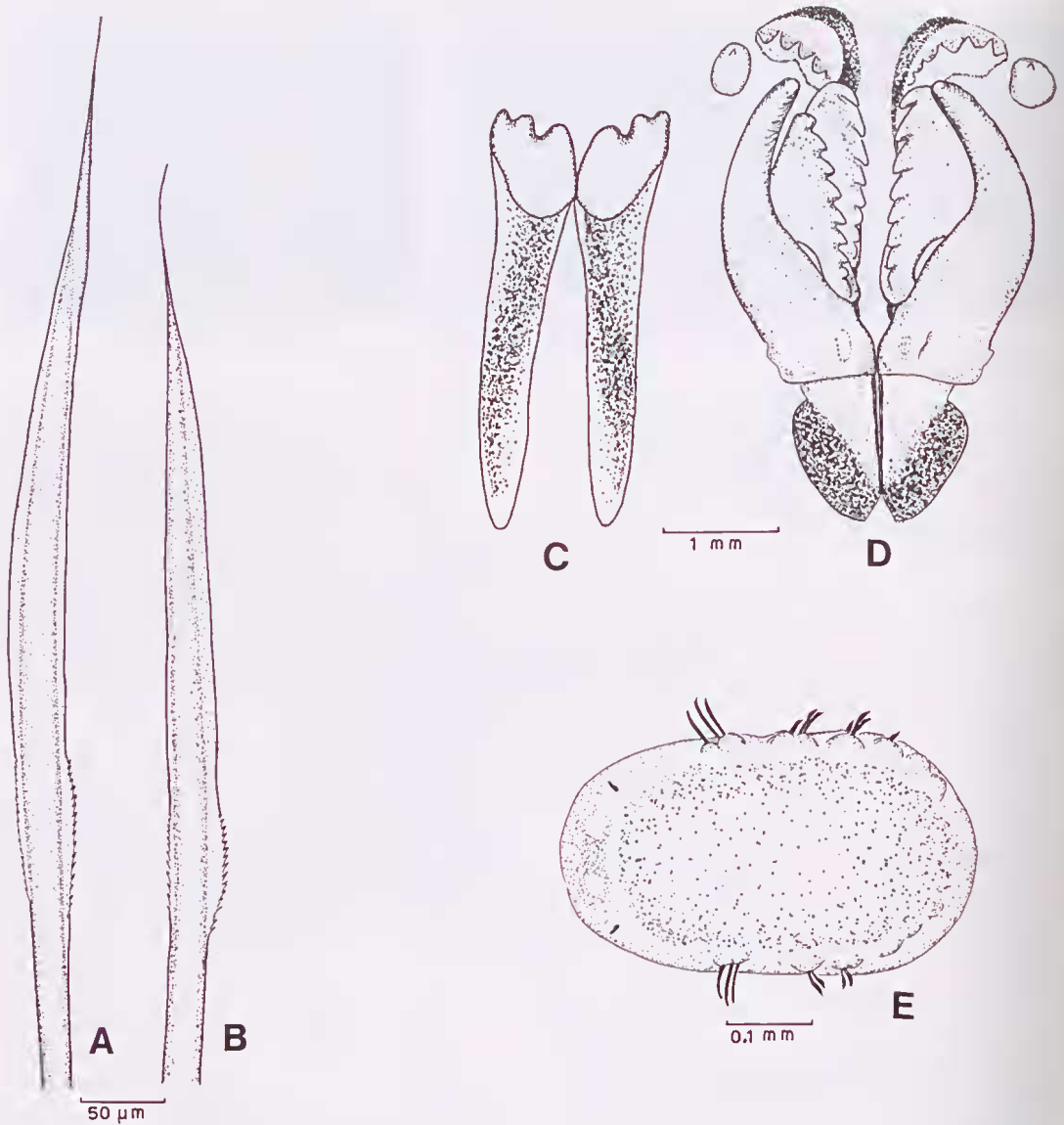


Fig. 15. *Diopatra maculata* sp. nov.: (A-B: holotype AM W19748; C-D: paratype AM W19746; E, paratype AM W19688). A, median limbate seta with swollen distal end from setiger 40; B, upper limbate seta from same; C, mandibles; D, maxillae; E, larva from jelly matrix covering distal part of tube.

pocket. Large hooks almost simple, others pseudocompound with short appendages and pointed hoods.

Unmodified parapodia (setiger 5 onwards) with pectinate and limbate setae. Pectinate setae (Fig. 12H) with 15-22 teeth in transverse combs; about 15-20 pectinate setae present per parapodium at setiger 40. Limbate setae (Fig. 15A, B) long, with wide, strongly serrated proximal shelves and wide wings, some with distal ends swollen (Fig. 15A). Lower limbate setae

replaced by 2 bidentate subacicular hooks from setiger 14 (13-18) depending on size (see Fig. 16 for range of all specimens examined).

Pygidium with slender anal cirri; dorsal pair about as long as last 4 setigers, ventral pair one third thereof.

Mandibles (Fig. 15C) with robust shafts and high calcareous cutting plates. Distal ends of cutting plates with two indentations each. Shafts darkly sclerotized, particularly in oblique stripe from outer proximal to inner distal parts. Maxil-

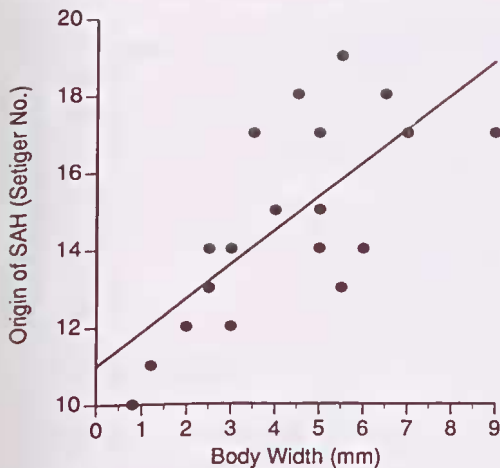


Fig. 16. *Diopatra maculata* sp. nov.: Relationship between body width of specimens and origin of subacicular hooks (SAH) [$r^2 = 0.504$, $y = 0.87x + 11.0$, $P < 0.0001$ (significance of overall regression)].

lae (Fig. 15D) moderately sclerotized but heavily calcified, giving them grey to brown colour, except for black attachment lamellae and black outer part of carriers. Maxillary formula (based on 5 types): Mx I = 1 + 1; Mx II = 7 (6-8) + 6 (6-8); Mx III = 6 (5-7) + 0; Mx IV = 6 (4-6) + 7 (6-7); Mx V = 1 + 1.

Tubes consisting of tough, parchment-like inner layer with an outer layer of muddy sand and occasional small pieces of vegetation and shells attached on angle, except for distal 4-5 cm where pieces are larger and closer together.

Etymology. In reference to the spotted pigmentation of the anterior part of the worm.

Remarks. *Diopatra maculata* is a member of the *D. amboinensis* complex (see Discussion). Of the five Australian species in the complex, it is the only one with falcate to weakly bidentate pseudocompound hooks; the hooks being clearly bidentate in the other four species.

Biology. The holotype contains ova (maximum diameter 350 μ m) in its body cavity. A paratype (AM W19688) contains a few eggs, indicating recent spawning. The recent spawn is enclosed in a mucous matrix which covers the outer distal part of the tube. The thousands of larvae are ovoid, have developed 3-4 pairs of parapodia, 2 eyespots, and measure about 500 x 300 μ m (Fig. 15E). Parapodia 1 to 3 can be distinguished as little lobes. Parapodium 1 bears three curved pointed setae; parapodia 2-4 bear three, two, and one short-tipped winged setae

respectively. In addition, each parapodium bears one acicula.

Distribution. Western Australia, Northern Territory, Queensland (Fig. 6); intertidal.

Diopatra oligopectinata, sp. nov.
(Figs 6, 17-19)

Type material. HOLOTYPE - WAM 62-79: incomplete specimen, with tube, 43 mm long (57 setigers), 6.0 mm wide, RV *Flinders*, NE of Garden Island, Cockburn Sound, Western Australia, 32°8.4'S, 115°40.6'E, seagrass, muddy sand, 29 November 1972 coll. L. Marsh. 5

PARATYPES - WAM 40-79: 2 incomplete specimens, 15-29 mm long (23-52 setigers), 3.5 - 4.0 mm wide. Western Australia, Sta. 21, Cockburn Sound, 28 February 1978 coll. F. Wells & C. Bryce. WAM 59-79: 1 incomplete specimen, 45 mm long (61 setigers), 5.5 mm wide, Western Australia, RV *Flinders* sta. 12, heading E off City Beach, 12 October 1976 coll. L. Marsh. WAM 60-79: 2 incomplete specimens. 24-28 mm long (34-35 setigers), 3-6 mm wide, Western Australia, RV *Sprightly* sta. 2M, about 8 km NW of Dongara, 29°16' to 14.5'S, 114°52' to 53.5'E, 13 m, 16 February 1976.

Additional material. WESTERN AUSTRALIA - WAM 39-79: 1 incomplete specimen in poor condition, Cockburn Sound.

All available specimens are incomplete; widths range from 3.0 to 6.0 mm.

Diagnosis. Antennal styles with brown specks; four pairs of modified parapodia with bidentate pseudocompound hooks with long to very long appendages; limbate setae with proximal shelves; few (2-8) transverse pectinate setae with few (6-11) teeth at setiger 40; mandibular shafts pale, darkened only medially.

Description. Colour markings absent on holotype and three paratypes, others with faded light brown specks on prostomium, palps, antennae, anterior parapodia and dorsum. Prostomium (Fig. 17A) anteriorly short and rounded with pair of subulate frontal palps. Ceratophores of antennae with 11-12 (9-12) proximal rings and a longer distal ring. Styles moderately long, tapering only slightly towards distal end, with blunt tips; posterior antennae about equally long, to setiger 15-16 (11-17), anterior laterals to 8 (4-8). Styles with 16-18 interrupted longitudinal rows of sensory buds. Buds flat; pores of serous glands forming semicircles (Fig. 18). Nuchal grooves forming 3/4 circles. Tentacular cirri stout, mod-

erately long, about 2 (1-2) times as long as peristomium; inserted slightly subdistally on moderately long peristomium, almost lateral to posterior lateral antennae.

Anterior parapodia with rounded to truncated presetal and subulate postsetal lobes (Fig. 17B). Presetal lobe present to about setiger 15, postsetal lobe becoming gradually smaller but remaining as distinct lobe toward end of fragments. Dorsal

cirri subulate, becoming more slender posteriorly; ventral cirri subulate on anterior 4 setigers. Spiralled branchiae (Fig. 17C) from setiger 5, best developed on setigers 7-10 with 10 (5-9) whorls, reaching to prostomium when extended anteriorly. Individual filaments relatively short and thick. Number of filaments decreasing gradually after setiger 10, single filaments from about setiger 50-60, absent shortly thereafter.

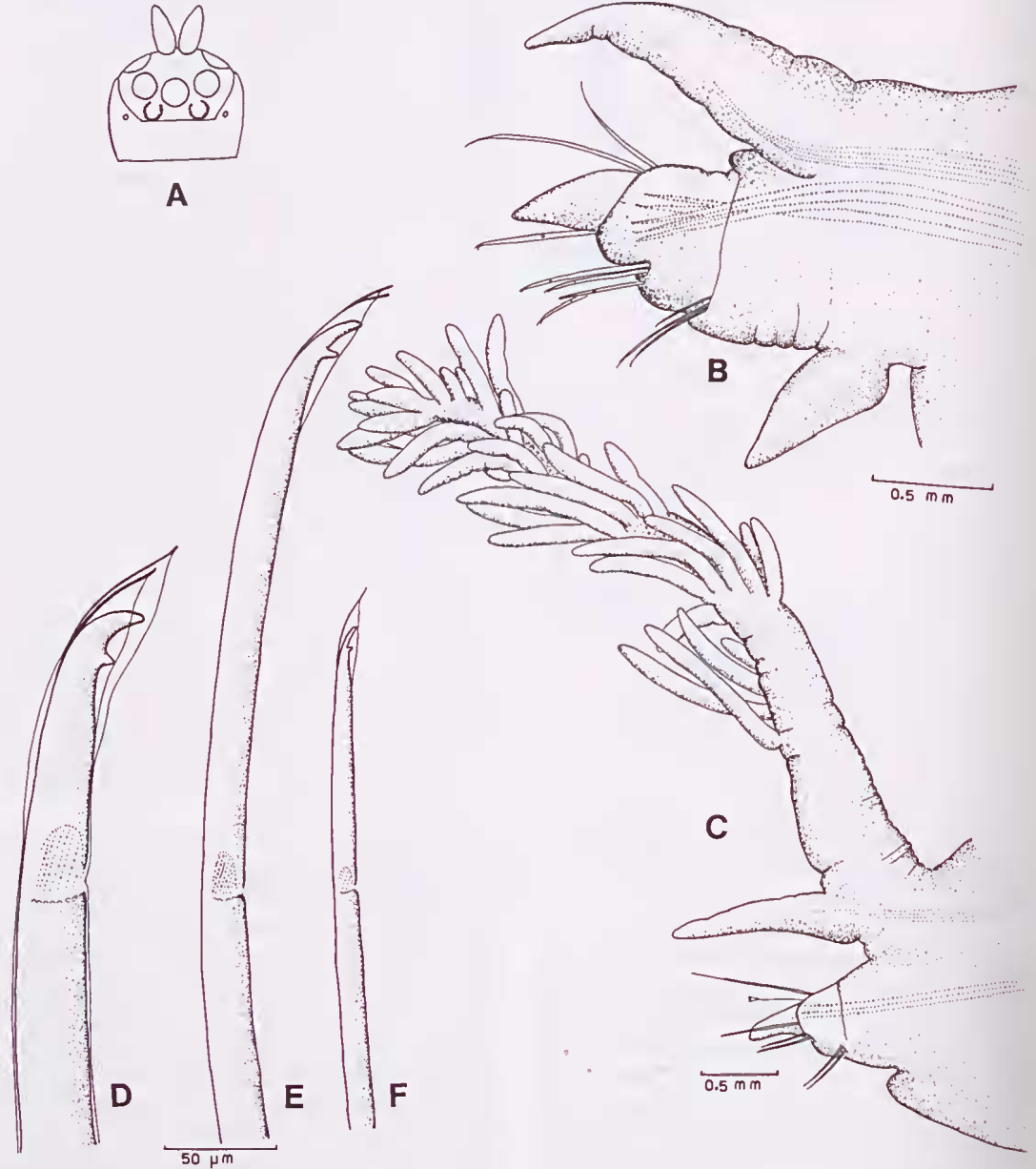


Fig. 17. *Diopatra oligopectinata* sp. nov.: (B-C: paratype, WAM 60-79; D-F: paratype, WAM 40-79). A, stylized diagram of prostomium and peristomium, dorsal view; B, parapodium 1, anterior view; C, parapodium 6, same view; D, large median pseudocompound hook from setiger 1; E, less robust pseudocompound hook from same; F, slender pseudocompound hook from same.

Modified parapodia (setigers 1-4) with 1-2 slender upper limbate setae and pseudocompound bidentate hooks with long to very long appendages and pointed hoods. Each parapodium with 1-2 large median (Fig. 17D) and 3-4 less robust hooks (Fig. 17E) projecting from main setal pocket, and 2-3 slender hooks (Fig. 17F) from small lower pocket.

Unmodified parapodia (setiger 5 onwards) with pectinate and limbate setae. Pectinate setae (Fig. 19A, B) from setiger 6 with 6-11 long teeth of varying widths in transverse combs; 5 (2-8) pectinate setae per parapodium at setiger 40. Limbate setae (Fig. 19C, D) with strongly serrated proximal shelves and wide wings. Lower limbate setae replaced by 2 bidentate subacicular hooks from setiger 14 (13-16).

Mandibles (Fig. 19E) lightly sclerotized, shafts only darkened medially and at edges of cutting plates; shafts medially thickened with thin lateral shelves; calcareous cutting plates high and with two distal indentations each. Maxillae (Fig. 19F) also relatively pale, darkest parts being carriers and attachment lamellae; maxillary formula (based on 5 types): Mx I = 1 + 1; Mx II = 7 (5-9) + 9 (6-9); Mx III = 9 (6-8) + 0; Mx IV = 6 (6-8) + 8 (8-10); Mx V = 1 + 1.

Tubes with tough, parchment-like inner layer and outer layer mainly of shell fragments, with a few other foreign particles attached at right angle in close circles, in *D. dentata*.

Etymology. The name of the new species is derived from its pectinate setae, which are few in number and have few teeth each.

Remarks. *Diopatra oligopectinata* belongs to the *D. amboinensis* complex (see Discussion). Of the five Australian species in the complex, it resembles *D. dentata* most with respect to the pseudocompound hooks, pectinate setae and tubes. However, *D. oligopectinata* can be distinguished from *D. dentata* by its shorter and thicker branchial filaments, and mandibles with paler

shafts and cutting plates with two indentations each.

Biology. None of the specimens contained gametes.

Distribution. Western Australia, Cockburn Sound and Dongara (Fig. 6); shallow depths.

Diopatra albimandibulata sp. nov.
(Figs 6, 20-22)

Type material. HOLOTYPE - AM W20367: incomplete specimen in 2 parts, 32+10 mm long (59+20 setigers), 3.5 mm wide, Abbot Point, Bowen, Queensland, 19°35'S, 148°04'E, 5 m, 10 June 1983 coll. J. Ottaway sta. 127. 43

PARATYPES - AM W20367: 1 incomplete specimen, 18 mm long (36 setigers), 3.5 mm wide, and 2 incomplete specimens left in tubes, same data as holotype; AM W20368: 2 complete specimens, 35-61 mm long (105-145 setigers), 2.0 mm wide and 22 incomplete specimens, 7-35 mm long (24-76 setigers), 1.8-3.5 mm wide, with tubes, same locality as holotype, 5.5-18.5 m, 10 June 1983, J. Ottaway sta. 122; AM W20372: 1 incomplete specimen, 18 mm long (39 setigers), 2.5 mm wide, with tube, same locality as holotype, 6-18 m, 16 June 1983, coll. J. Ottaway sta. 115; AM W20373: 15 incomplete specimens, 9-30 mm long (18-52 setigers), 1.0-3.0 mm wide, with tubes (5 with egg sacs), same locality as holotype, 5 m, 10 June 1983, coll. J. Ottaway sta. 112.

The only two complete specimens are immature, measuring 35-61 mm long (105-145 setigers), and 2.0 mm wide. The greatest width of incomplete specimens is 3.5 mm.

Diagnosis. Antennal styles with median brown band; four pairs of modified parapodia with bidentate pseudocompound hooks with moderately long appendages; limbate setae with proximal shelves; 5-8 transverse pectinate setae with 18-24 teeth each at setiger 40; mandibular shafts white.

Description. Colour pattern (faded in some specimens) consisting of irregular light brown specks on prostomium, frontal palps, ceratophores and anterior part of dorsum; median part of styles with wide transverse brown band.

Prostomium (Fig. 20A) anteriorly short and rounded with subulate frontal palps slightly separated from each other. Ceratophores of antennae with 10-11(8-11) proximal rings and a longer distal ring, styles long, tapering towards distal end, ending bluntly. Posterior antennae about equal in length to setiger 15-16 (14-24), anterior laterals to 10(9-16). Styles with 16-18 inter-



Fig. 18. Scanning electron micrograph of sensory buds of antenna of *Diopatra oligopectinata* sp. nov. (scale 5 µm).

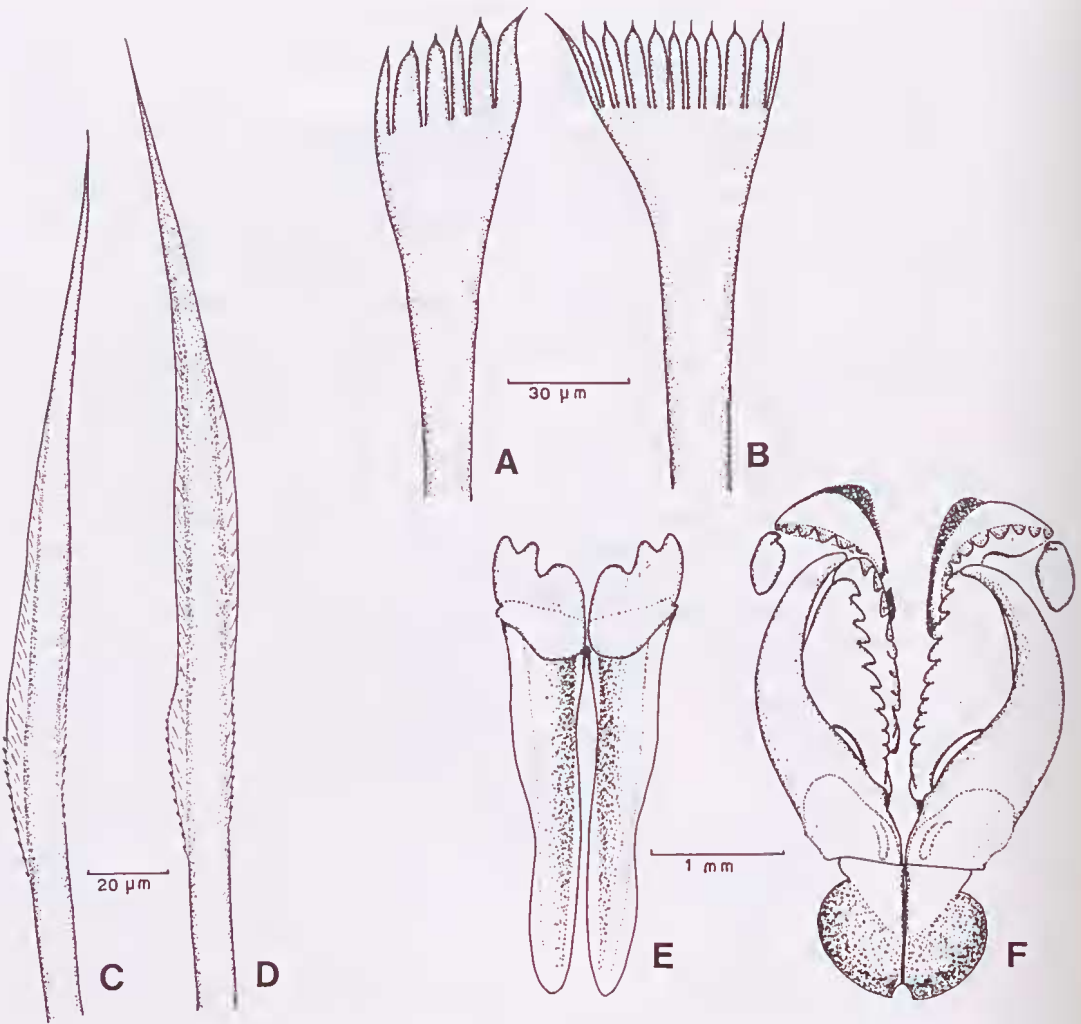


Fig. 19. *Diopatra oligopectinata* sp. nov.: (A-D: paratype, WAM 60-79; E, F: paratype, WAM 59-79). A, pectinate seta with 6 teeth from setiger 6; B, same with 11 teeth from setiger 34; C, upper limbate seta from same; D, median limbate seta from same; E, mandibles; F, maxillae.

rupted longitudinal rows of sensory buds. Buds flat, pores of serous glands forming semicircle (Fig. 21). Nuchal grooves forming semicircles. Tentacular cirri moderately long, about 2 (2-3) times length of peristomium; inserted subdistally on short peristomium, almost lateral to posterior lateral antennae.

Anterior parapodia with truncated presetal lobe and subulate postsetal lobe (Fig. 20B). Presetal lobe present to setiger 6, postsetal lobe very reduced by setiger 40, insignificant in posterior segments. Dorsal cirri relatively long, subulate, becoming more slender posteriorly; ventral cirri subulate on anterior 4(4-5) setigers. Spiralled branchiae (Fig. 20C) from setiger 5(4-5), best developed on setigers 7-10, with 8(5-8)

whorls, reaching to ceratophores when extended anteriorly. Individual filaments short and slender. Number of filaments decreasing gradually after setiger 10, single filaments from setiger 48(30-44).

Modified parapodia (setigers 1-4) with 1-2 slender upper limbate setae and bidentate pseudocompound hooks with moderately long appendages and short to slightly pointed hoods. Each parapodium with 1 large median (Fig. 20D) and 2-3 less robust hooks (Fig. 20E) projecting from main setal pocket, and 2-3 slender hooks (Fig. 20F) from small lower pocket.

Unmodified parapodia (setiger 5 onwards) with pectinate and limbate setae. Pectinate setae (Fig. 20G) with 18-24 teeth in transverse combs;

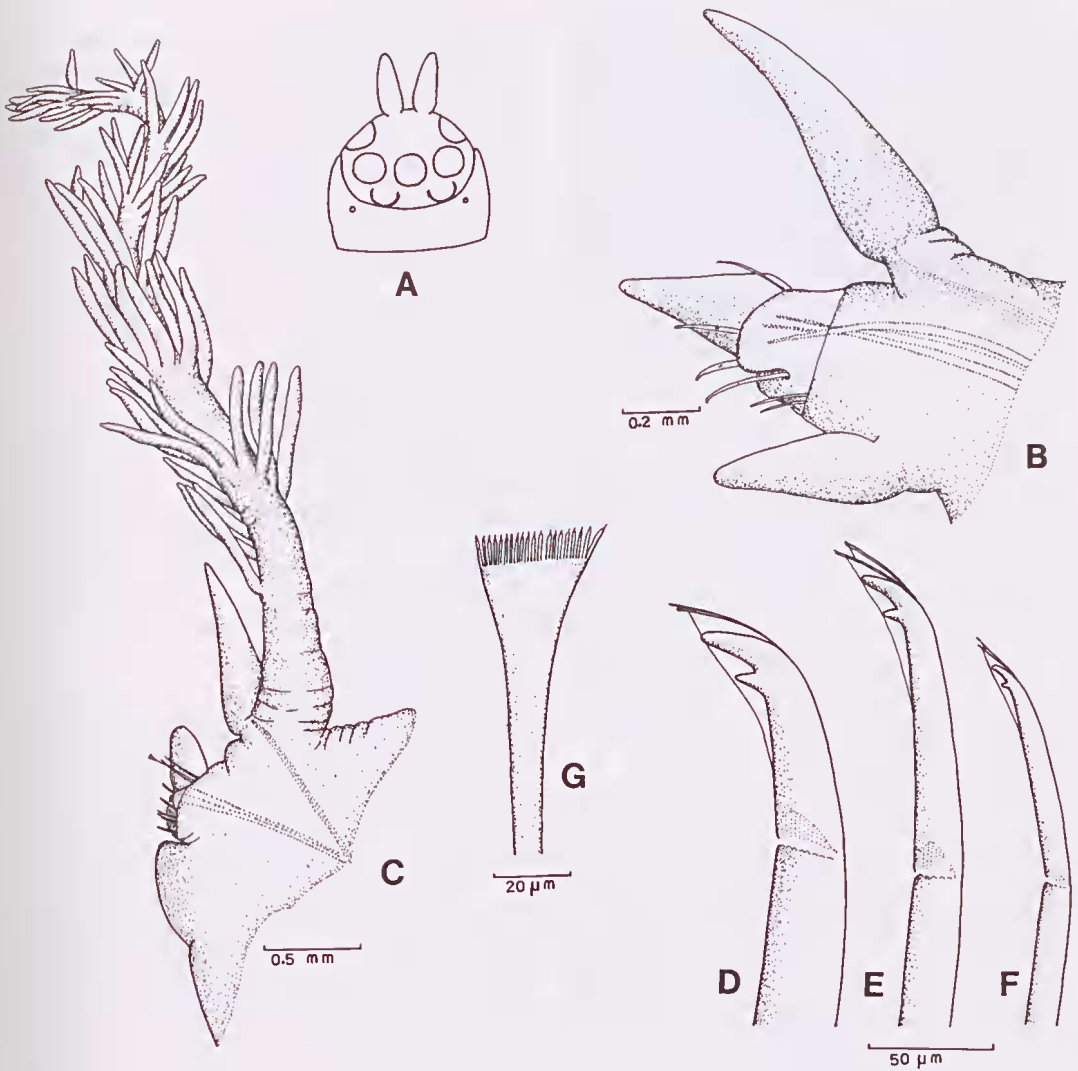


Fig. 20. *Diopatra albimandibulata* sp. nov.: Holotype, AM W20367. A, stylized diagram of prostomium and peristomium, dorsal view; B, parapodium 1, anterior view; C, parapodium 6, same view; D, large median pseudocompound hook from setiger 1; E, less robust pseudocompound hook from same; F, slender pseudocompound hook from same; G, pectinate seta from setiger 40.

about 4-8 pectinate setae present per parapodium at setiger 40. Limbate setae (Fig. 22A, B) with serrated proximal shelves and narrow wings. Lower limbate setae replaced by 2 bidentate subacicular hooks from setiger 13(11-15).

Pygidium with slender anal cirri; dorsal pair about as long as last 4-6 setigers, ventral pair 1/3 to 1/2 as long.

Mandibles (Fig. 22C) with slender shafts and high calcareous cutting plates. Distal ends of cutting plates with one deep incision (close to median fusion) and one indistinct lateral incision each. Shafts strongly calcified, white, ex-

cept for area of distal fusion, where some sclerotization is visible. Maxillae (Fig. 22D) light brown, except for black carriers and attachment lamellae. Maxillary formula (based on seven paratypes of which one has symmetrical maxillae III, i.e. both left and right present): Mx I = 1 + 1; Mx II = 7 (6-9) + 8 (6-8); Mx III = 7 (6-8) + 0(0-8); Mx IV = 8 (6-9) + 9 (6-8); Mx V = 1 + 1.

Tubes consisting of relatively soft, parchment-like inner layer, with an outer layer mainly of small shells and shell fragments attached at angle in close circles.

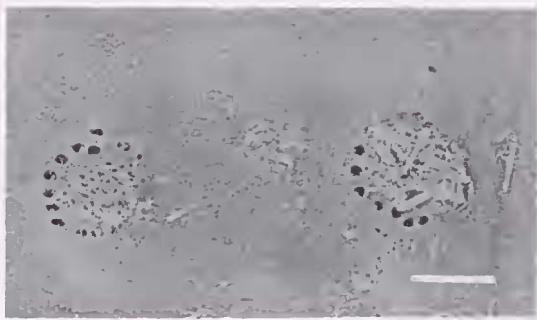


Fig. 21. Scanning electron micrograph of sensory buds of antenna of *Diopatra albimandibulata* sp. nov. (scale 5 μ m).

Etymology. In reference to the white mandibles.

Remarks. *D. albimandibulata* is a member of the *D. amboinensis* complex (see Discussion). Of the five Australian species in the complex, *D. albimandibulata* most closely resembles *D. oligopectinata* with respect to the short branchial filaments, similar pseudocompound hooks, and few pectinate setae. It can be distinguished from *D. oligopectinata* most easily by its slender white mandibles; those of the latter having outer lateral shelves and brown inner edges.

Biology. Specimens from sta. 112 (AM W20373) were brooding; five tubes were each found to have a small egg sac attached to their distal ends, directed towards the lumen of the tube. The sacs are globular, measure 3.0 to 4.5 mm in diameter and contain about 250 3-setiger larvae enclosed by a mucous envelope. The larvae are oval and measure 300-330 x 240-260 μ m.

Distribution. The new species is only known from Bowen, Queensland (Fig. 6); 5-18.5 m.

Diopatra lilliputiana sp. nov.

(Figs 6, 23-26, Table 1)

?*Diopatra* sp. (?*dentata*) - Augener 1913:281 (Shark Bay, Western Australia).

Type material. HOLOTYPE - AM W19691: incomplete specimen, 11 mm long (36 setigers), 1.6 mm wide, Enderby Island, Danpier Archipelago, Western Australia, 20°36'S, 116°30'E, mangroves, 31 March 1987, coll. P. Hutchings. 6

PARATYPES - AM W20562: 1 complete specimen with tube, 31 mm long (125 setigers), 1.2 mm wide, same data as holotype; WAM 182-86: 1 incomplete specimen, with tube and 7-setiger larvae, 21 mm long (67 setigers), 1.2 mm wide, Western Australia, Bay of Rest, North West Cape, September 1981, coll. F. Wells & C.

Bryce; WAM 187-86: 1 incomplete specimen, with tube and egg sac, and additional tube with 15-setiger larvac, 8 mm long (34 setigers), 1.1 mm wide, data as above; WAM 188-86: 1 incomplete specimen, with tube and eggs, and larger empty tube, 19 mm long (66 setigers), 1.3 mm wide, data as above; WAM 190-86: 1 incomplete male specimen, with tube, and 2 additional tubes, 1 with eggs and 1 with 15-setiger larvae, data as above; NTM W2135: 1 incomplete specimen, with tube, 15 mm long (51 setigers), 2.0 mm wide, Western Australia, Broome, 2 October 1984, coll. R. Hanley.

The only complete specimen measures 31 mm in length (125 setigers), 1.2 mm wide; incomplete specimens range in width from 1.0-2.0 mm.

Diagnosis. Very small species; antennal styles with brown band; three to four pairs of modified parapodia with bidentate and falcate pseudocompound hooks with short appendages; limbate setae without proximal shelves; 3-5 slightly oblique pectinate setae with 25-30 teeth each at setiger 40.

Description. Animals white, with brown specks on prostomium and anterior part of body; middle to distal third of antennal styles with brown band, sometimes faded. Prostomium (Figs. 23A, 24A) anteriorly rounded, with oval to subulate frontal palps. Cceratophores of anterior antennae with 5-6, and posterior antennae with 6-8, proximal rings plus a longer distal ring. Styles relatively short, becoming slightly slenderer towards distal end, ending in blunt tips; posterior antennae about equal in length to setiger 9-10 (6-13), anterior laterals to 3 (2-4). Styles with 10-12 interrupted longitudinal rows of sensory buds. Buds flat, scrous openings forming semicircles (Fig. 24B). Nuchal grooves forming shallow crescents. Tentacular cirri about 1 (1-2) times as long as peristomium; inserted slightly subdistally on short peristomium, almost lateral to posterior lateral antennae.

Anterior parapodia with distally narrowing presetal lobe and large subulate postsetal lobe (Fig. 23B). Presetal lobe present to setiger 4-5, postsetal lobe decreasing rapidly in size after setiger 5, but remaining as small boss to setiger 30-40. Dorsal cirri subulate, becoming more slender posteriorly; ventral cirri subulate on anterior 3-4 setigers. Spiralled branchiae (Fig. 23C) from setiger 5 (4-5), first two pairs best developed with 4-5 whorls, reaching to setiger 1 or peristomium when extended anteriorly, decreasing gradually in size after setiger 6-7.

Branchial filaments short and slender, single from setiger 26-37, absent shortly thereafter.

Modified parapodia [setigers 1-4 (1-3 or 4)] with 1-2 slender upper limbate setae and bidentate and falcate pseudocompound hooks. Each parapodium with 1 large median (Fig. 23D, E) and 1-3 less robust hooks (Fig. 23F) projecting from main setal pocket, and 1-2 slender hooks from small lower pocket. Large median hook short appendaged, others with moderately long appendage with short hoods.

Unmodified parapodia (setiger 4-5 onwards) with slender, almost smooth limbate setae with narrow wings (Fig. 23G). Pectinate setae (Fig. 23H) with 25-30 long teeth in slightly oblique combs; 3-5 pectinate setae present per parapodium at setiger 30-40. Lower limbate setae replaced by 2 bidentate subacicular hooks from setiger 14(10-12).

Pygidium with short anal cirri; dorsal pair about as long as last three setigers, ventral pair half as long.

Mandibles lightly sclerotized, shafts darkened laterally only; shafts slender, calcareous cutting plates high, with one distal indentation each (Fig. 25A). Maxillae also very pale, darkest parts being basal edge of carriers and attachment lamellae (Fig. 25B). Falcate arch of Mx I medially extended in larger specimens, left MxII and III proximally equal in length. Maxillary formula (based on three paratypes): Mx I = 1+1; Mx II = (8-10)+(8-9); Mx III = (9-10)+0; Mx IV = (6-7)+(9-10); Mx V = 1+1.

Tubes consisting of soft inner layer with foreign particles, e.g. mud, sand and shell fragments, attached to the outside. Shells generally attached at angle, except a few larger ones which are flat against the tube. An apparently complete tube measures 33 mm in length.

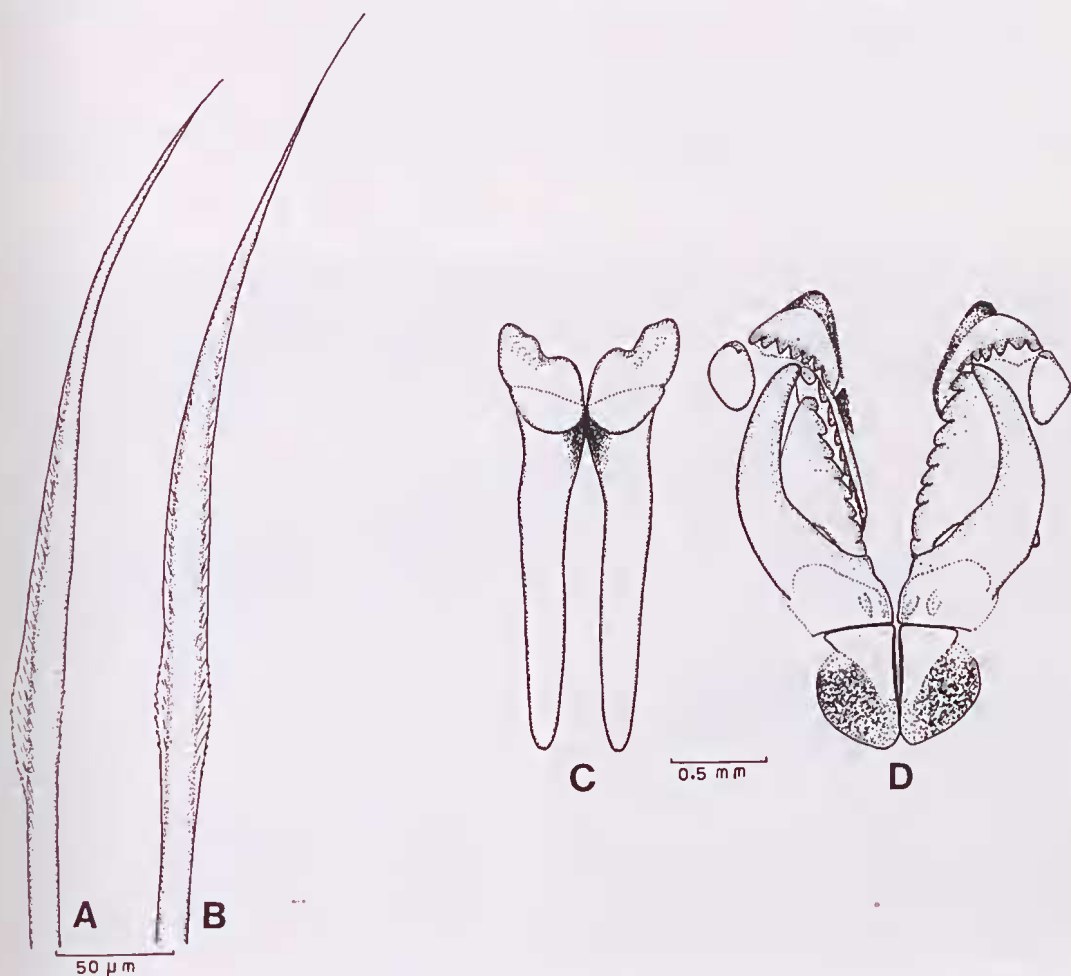


Fig. 22. *Diopatra albimandibulata* sp. nov.: (A-B: holotype, AM W20367; C-D: paratype, AM W20368). A, upper limbate seta from setiger 40; B, median limbate seta from same; C, mandibles; D, maxillae.

Etymology. The name is an allusion to the unusually small size of the new species, suggested by Swift's *Gulliver's Travels*.

Remarks. *Diopatra lilliputiana* resembles *D. hanleyi* n. sp. and *D. gigova* n. sp. in having similar pectinate and limbate setae. *Diopatra hanleyi* n. sp. can be distinguished by its brown pigmentation on the presetal lobes and at the bases of the dorsal cirri of the anterior parapodia. Furthermore, its large anterior hooks are simple.

While the mandibles of both *D. lilliputiana* and *D. gigova* n. sp. have calcareous plates with one deep indentation, the shafts of the former are only laterally darkened, while those of the latter are almost black except for their proximal tips.

The small specimen reported by Augener (1913:281) from Shark Bay, Western Australia, may belong to this species.

Biology. Although all of the specimens are sexually mature, some are smaller (1.0-1.1 mm

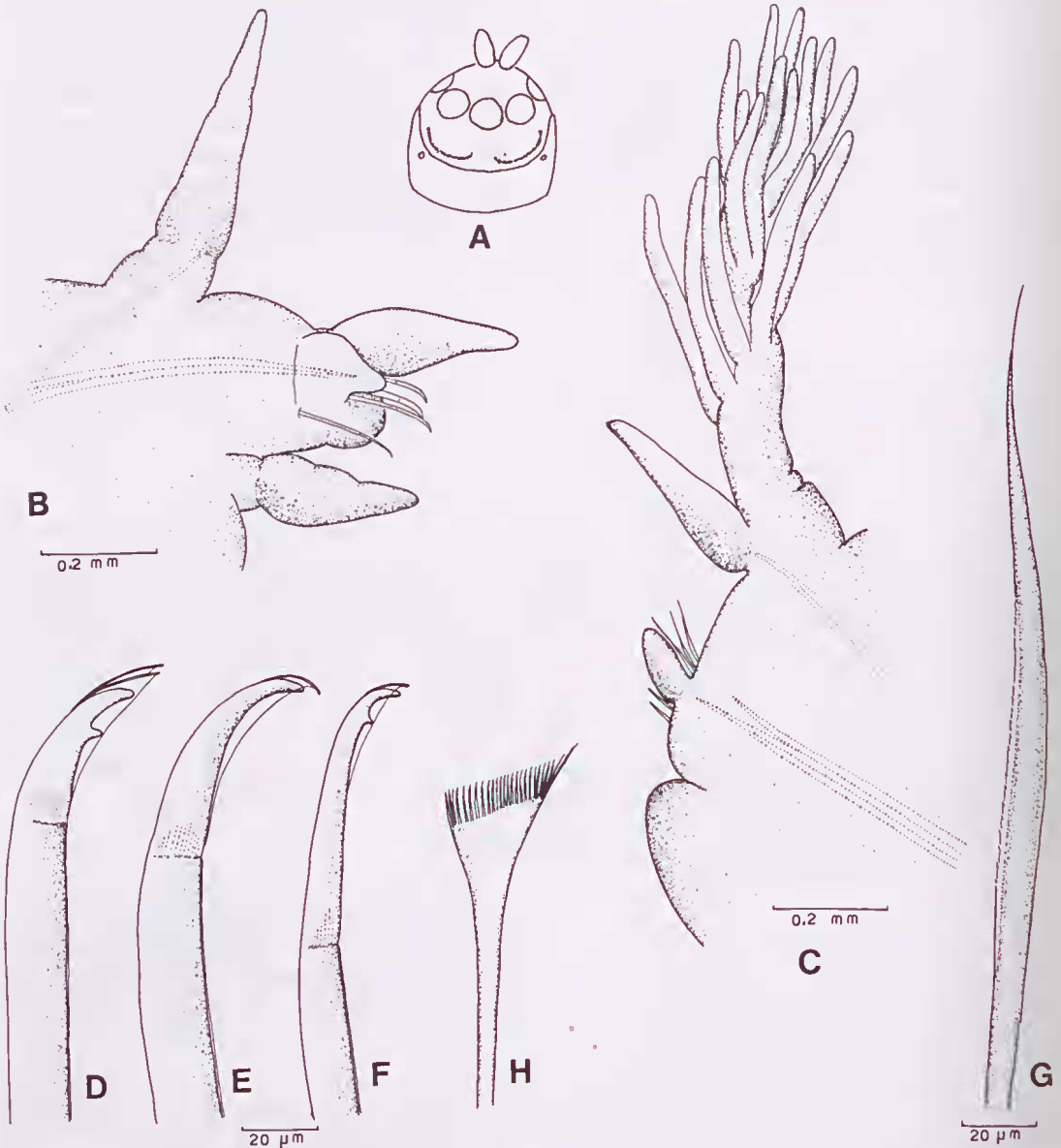


Fig. 23. *Diopatra lilliputiana* sp. nov.: Paratypes, WAM 187-86. A, stylized diagram of prostomium and peristomium, dorsal view; B, parapodium 2, anterior view; C, parapodium 6, posterior view; D, large median bidentate pseudo-compound hook from setiger 4; E, large median falcate pseudo-compound hook from setiger 2; F, less robust pseudo-compound hook from same; G, median limbate seta from setiger 40; H, pectinate seta from same.

wide) and presumably younger than others (1.2–2.0 mm wide). The former will here be referred to as ‘young adults’ and the latter as ‘adults’. The jaws are less sclerotized and calcified in the young adults. The most obvious difference is that the initial part of the mandible (the juvenile mandible) is still clearly visible in young adults due to very light calcification (Fig. 25C), the maxillae show almost no sclerotization and the falcate arch of the Mx1 is not medially extended (Fig. 25D).

One young adult (WAM 190-86) is a male. The coelom is distended with sperm from setiger 35 to the end of the fragment. The female specimens from the North West Cape were all brooding in their tubes. The stages present are: recently laid eggs, 7 and 15-setiger larvae.

The tube of one young adult (WAM 187-86) contains about 40 eggs of about 400 μm diameter. The eggs are enclosed in a delicate mucous sac, about 6 mm long. The tube of an adult (WAM 188-86) contains a broken egg sac with only 7–8 eggs. These are larger (about 800 $\times$ 600 μm), ovoid and have presumably started development. This female has also about 10 large (700 $\times$ 500 μm) eggs in its body cavity from setiger 60 to 66 (the end of the fragment), while another

adult female (NTM W2135) has eggs in its body cavity measuring 900 $\times$ 650 μm .

The tube of an adult (WAM 182-86) contains six 7-setiger larvae (Fig. 24C) measuring about 750 μm in length. They are spindle-shaped with a round prostomium and tapered posterior end with the greatest width (about 350 μm) at setigers 1–4. The prostomium is clearly delineated, lacking frontal palps but bearing five rudimentary antennae. Anterior lateral antennae are least developed, evident only as rounded protrusions. Posterior antennae are short and ovoid, ceratophores still absent. The peristomium and tentacular cirri are not yet developed. The first pair of parapodia is well developed with distinct dorsal and ventral cirri. Remaining parapodia are successively smaller, the last being only slight protrusions. Setae include, in addition to one acicula, curved pointed setae (Fig. 26A) on setiger 1; short-tipped winged setae (Fig. 26B) from setiger 2–6; setiger 7 has one acicula only (Table 1). Two small anal cirri are present.

About thirty 15-setiger larvae were found in the tube of a young adult (WAM 187-86). Larvae are all enclosed in a mucous sac about 7 mm long, their heads all facing in the same direction. The larvae (Fig. 24D) measure about 1500 μm in

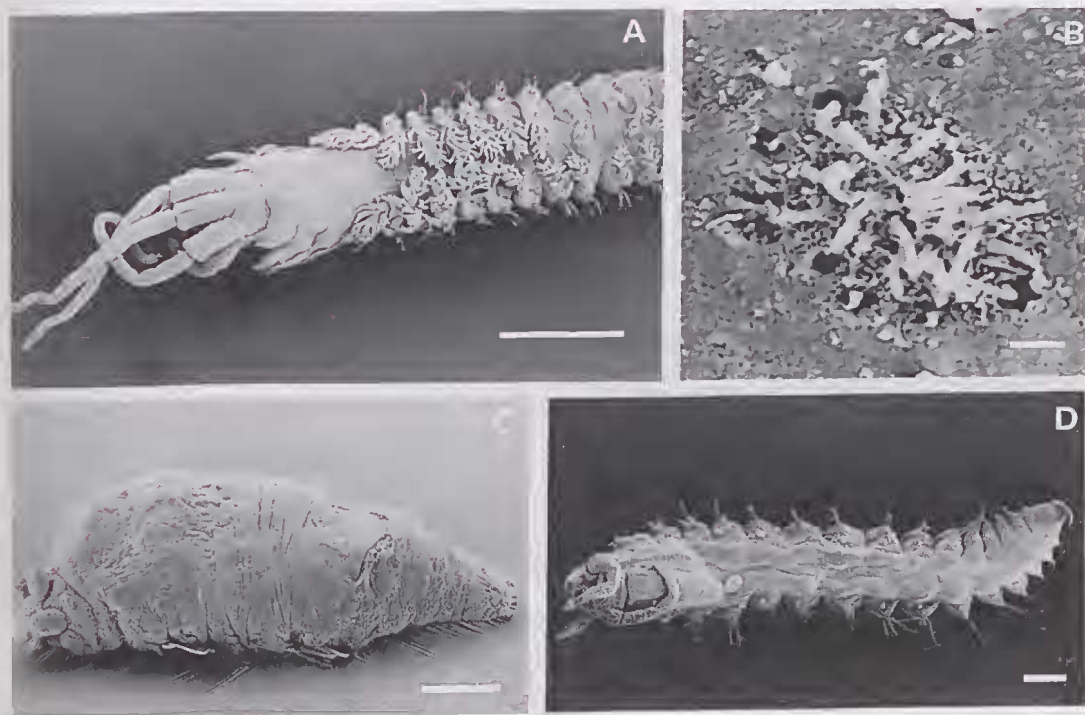


Fig. 24. Scanning electron micrographs of *Diopatra lilliputiana* sp. nov.: A, anterior part of body of ‘young adult’, dorsal view (scale 1 mm); B, sensory bud of antenna of same (scale 1 μm); C, 7-setiger larva, lateral view (scale 100 μm); D, 15-setiger larva, dorsal view (scale 100 μm).

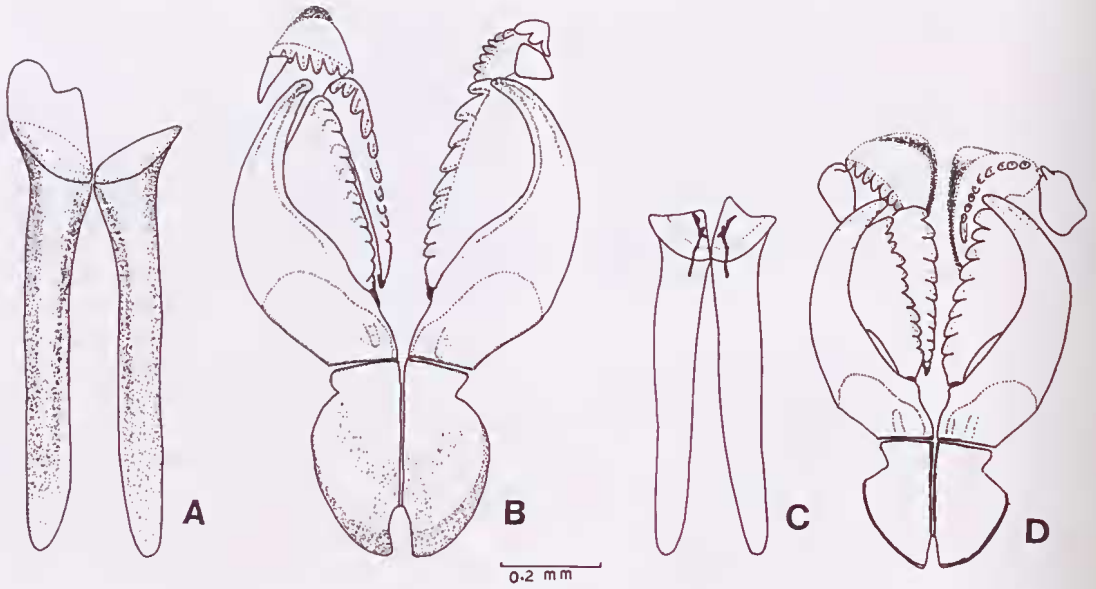


Fig. 25. *Diopatra lilliputiana* sp. nov.: Paratypes, WAM 187-86. A, mandibles of 'adult'; B, maxillae of same; C, mandibles of 'young adult'; D, maxillae of same.

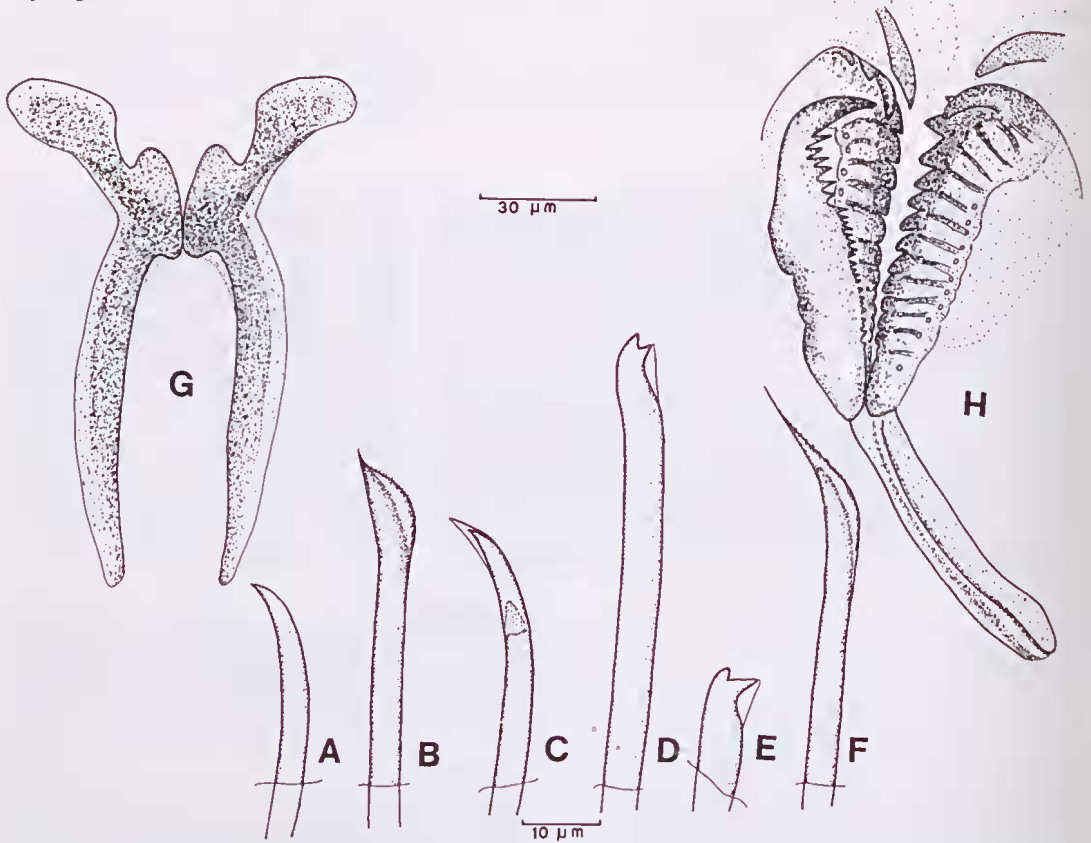


Fig. 26. *Diopatra lilliputiana* sp. nov.: (A-B: larvae associated with paratypes WAM 187-86; C-H: larvae of paratype WAM 182-86). A, curved pointed seta from setiger 1 of 7-setiger larva; B, short-tipped winged seta from setiger 4 of same; C, pseudocompound hook from setiger 1 of 15-setiger larva; D, long subacicular hook from setiger 6 of same; E, short subacicular hook from setiger 14 of same; F, long-tipped winged seta from setiger 6 of same; G, mandibles of same; H, maxillae of same.

length and 250 µm in width with parapodia. Their general appearance approaches that of the adults. Their prostomium bears frontal and labial palps and long antennae (to setiger 3) with indistinctly annulated ceratophores. Tentacular cirri are still absent. Dorsal cirri are present on setigers 1-13, cirriform ventral cirri on setigers 1-2.

Setiger 1 has three falcate pseudocompound hooks (Fig. 26C) and one curved pointed seta. Setigers 2-5 each bear three short-tipped winged setae and one limbate seta. From setiger 6 there is only one short-tipped winged seta, one long-tipped winged seta (Fig. 26F) and the first subacicular hook (Fig. 26D). Subacicular hooks become progressively shorter until they have the length and appearance of adult hooks (Fig. 26E) (Table 1). The anal cirri consist now of a pair of digitiform dorsal and a pair of short round ventral ones. The larval jaws are typical of the family with H-shaped mandibles (Fig. 26G) and maxillae (Fig. 26H) consisting of narrow carriers, a single left MxI with small proximal and larger distal teeth, a pair of MxII consisting of two large serrated plates, and an additional pair of ridges representing Mx IV.

Distribution. Broome, Enderby Island, Dampier Archipelago, North West Cape and probably Shark Bay, Western Australia (Fig. 6); intertidal.

Diopatra hanleyi sp. nov.

(Figs 6, 27, 28)

Type material. HOLOTYPE - NTM W4612: incomplete specimen in two parts, ovigerous, anterior part 34 mm long (66 setigers), 2.5 mm wide, Ludmilla Creek mouth, Darwin, Northern Territory, LWS, 18 February 1987, coll. R. Hanley.

3 PARATYPES - NTM W1127: 1 incomplete specimen, 50 mm long (160 setigers), 2.5 mm wide, Northern Territory, Cameron's Beach, Darwin, mangrove; NTM W3827: 2 incomplete specimens, with tubes, 57-65 mm long (116-135 setigers), 2.0 mm wide, Northern Territory, Lee Point, Darwin, LWS, rocky, stony reef, 12 February 1986, coll. R. Hanley.

All available specimens are incomplete; widths range from 2.0 to 2.5 mm.

Diagnosis. Antennal styles with brown specks; brown pigmentation on presetal lobes and bases of dorsal cirri; four to five pairs of modified parapodia with bidentate pseudocompound and simple hooks; limbate setae without proximal shelves; 3-14 transverse pectinate setae with 20-25 teeth at setiger 40.

Description. Species with striking colour pattern. Anterior part of body brownish except for white dorsal and ventral cirri and postsetal lobes. Additional darker brown pigmentation on prostomium, as rings on ceratophores and patches on presetal lobes and bases of dorsal cirri. One paratype (NTM W1127) is dark flesh-coloured and lacks the typical pigmentation.

Prostomium (Fig. 27A) anteriorly short and rounded with subulate frontal palps separated by gap. Ceratophores of antennae with 9 (7-8) proximal rings and a longer distal ring. Styles relatively short, tapering towards distal end; posterior antennae about equal in length to setiger 10-11 (10-13), anterior laterals to 3 (3-5). Styles with 16-18 interrupted longitudinal rows of slightly raised sensory buds (details of buds not clear in the only preparation). Nuchal grooves forming crescents. Tentacular cirri moderately long, about 1.5 times as long as peristomium; inserted slightly subdistally on short peristomium, almost lateral to posterior lateral antennae.

Table 1. Setal composition of two larval stages of *Diopatra lilliputiana*. Letters represent setal types: p, curved pointed seta (Fig. 26A); a, short-tipped winged seta (Fig. 26B); A, aciculum; H, pseudocompound hooded hook (Fig. 26C); L, limbate seta; b, long-tipped winged seta (Fig. 26F); S, subacicular hooded hook (Fig. 26D, E). Lower cases indicate provisional (larval setal types), capitals indicate permanent (adult) types. Numbers represent number of each setal type on each parapodium.

Stage	Setiger Number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
7-Setiger	3p 1A	3a 1A	3a 1A	3a 1A	2a 1A	1a 1A	1A								
15-setiger	3H 1p	1L 3a	1L 3a	1L 3a	1L 3a	1L 1a	1L 1b	1L 1b	2L	2L	2L	2L	1L	1L	
	1A	1A	1A	1A	1A	1A 1S	1A 2S	1A 2S	1A 2S	1A 2S	1A 2S	1A 2S	1A 1S	1A 1S	1A

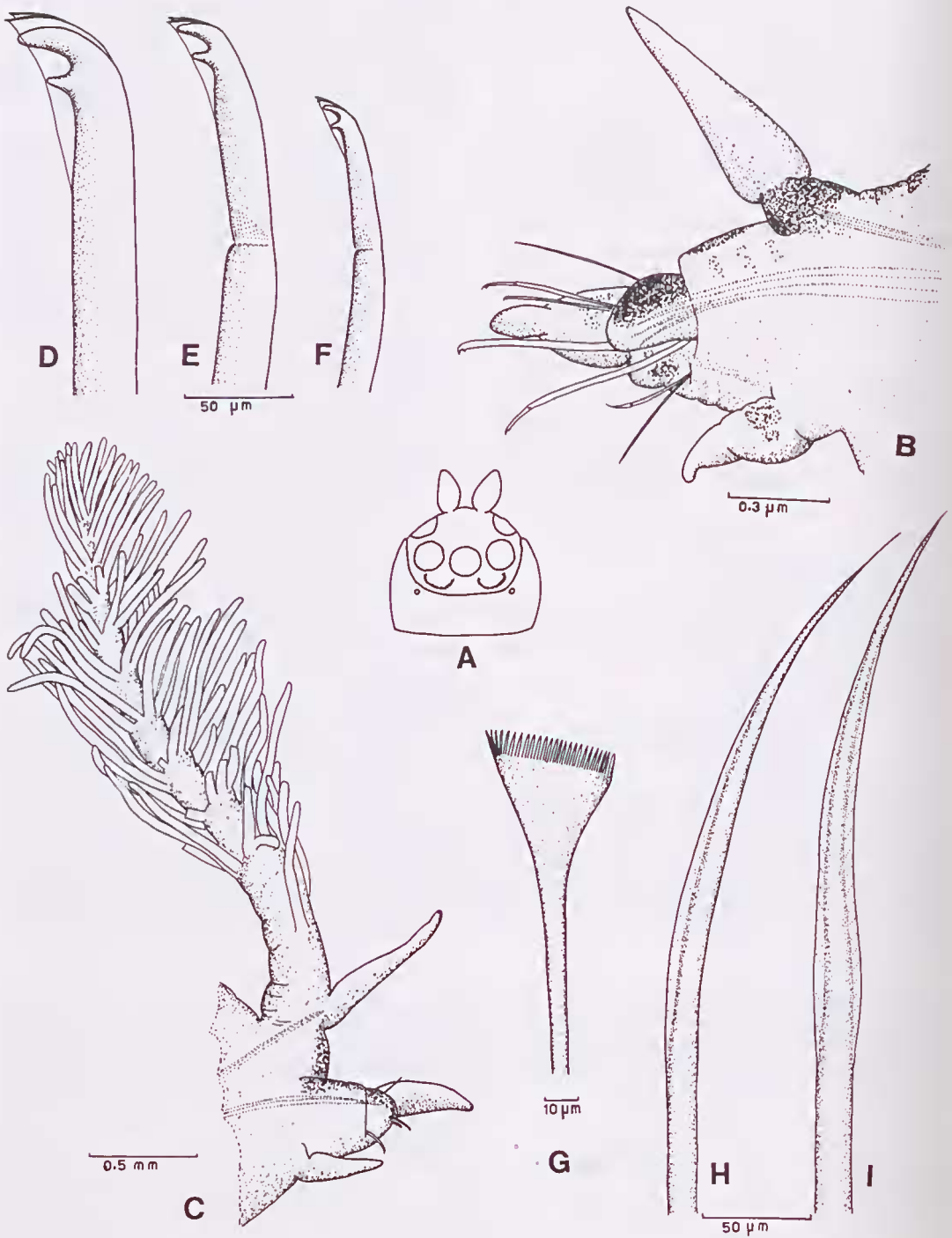


Fig. 27. *Diopatra hanleyi* sp. nov.: (Holotype NTM W4612). A, stylized diagram of prostomium and peristomium, dorsal view; B, parapodium 1, anterior view; C, parapodium 5, same view; D, large simple median hook from setiger 1; E, less robust pseudocompound hook from same; F, slender pseudocompound hook from same; G, pectinate seta from setiger 40; H, upper limbate seta from same; I, median limbate seta from same.

Anterior parapodia with oval, lip-like presetal and subulate postsetal lobes (Fig. 27B). Presetal lobes present to setiger 6-8, postsetal lobes decreasing to small lip by setiger 40, absent from median region. Dorsal cirri subulate, becoming more slender posteriorly; ventral cirri subulate on anterior 4 (4-6) setigers. Spiralled branchiae (Fig. 27C) from setiger 4 (4-5), best developed on setigers 4-8, with up to 11 (6-12) whorls, reaching to ceratophores (setiger 1 to peristomium) when extended anteriorly. Individual filaments long and slender. Number of filaments decreasing gradually, single filaments from setiger 54 (50-60), absent shortly thereafter.

Modified parapodia [setigers 1-5 (1-4 to 1-6)] with 1-2 slender upper limbate setae and bidentate hooks with short hood. Each parapodium with 1 large median (Fig. 27D) and 2-3 less robust hooks (Fig. 27E) projecting from main setal pocket, and 1-2 slender hooks (Figs. 27F) from small lower pocket. Large hook simple, all others pseudocompound with moderately long appendages.

Unmodified parapodia (setiger 5 to 7 onwards) with pectinate and limbate setae. Pectinate setae with 20-25 short teeth in transverse combs (Fig. 27G); 14 (3-13) pectinate setae present per parapodium at setiger 40. Limbate setae (Fig. 27H, I) almost smooth with narrow wings. Lower limbate setae replaced by 2 bidentate subacicular hooks from setiger 17 (16-18).

Mandibles (Fig. 28A) with moderately dark, slender shafts. Calcareous cutting plates each with two distal indentations. Maxillae (Fig. 28B) strongly sclerotized, dark brown; Mx I with medially extended falcate arch and proximally long Mx III. Maxillary formula (based on holotype and one paratype): Mx I = 1 + 1; Mx II = 8 (7) + 8(7); Mx III = 7 (7) + 0; Mx IV = 5 (7) + 9 (8); Mx V = 1 + 1.

Tubes consisting of relatively soft inner layer with outer layer of sand and relatively long pieces of vegetation attached at angle, giving it a ragged appearance.

Etymology. It gives me pleasure to name the new species in honour of Dr. Russell Hanley.

Remarks. The affinities of *D. hanleyi* have been discussed above (see remarks for *D. liliputiana*).

Biology. The body cavity of the holotype is tightly packed with ova from about setiger 50 onwards. The largest ova measure 170 μ m in diameter. The two paratypes are relatively young

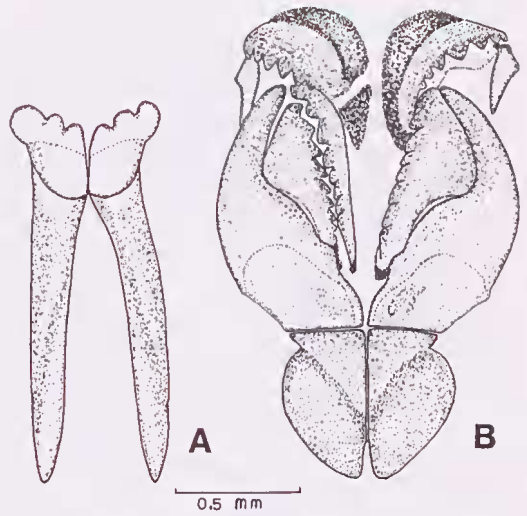


Fig. 28. *Diopatra hanleyi* sp. nov.: (Holotype NTM W4612). A, mandibles; B, maxillae.

specimens as evidenced by their smaller width, shorter branchiae and paler maxillae.

Distribution. *Diopatra hanleyi* is known only from Darwin, Northern Territory (Fig. 6); intertidal.

***Diopatra gigova* sp. nov.**
(Figs 6, 29, 30)

Type material. HOLOTYPE - AM W19692: complete specimen with tube and attached egg sac, 45 mm long (98 setigers), 3.5 mm wide, below hut, Enderby Island, Dampier Archipelago, Western Australia, 20°36'S, 116°30'E, intertidal, 27 March 1987, coll. P. Hutchings.

1 PARATYPE - AM W20563: incomplete specimen, with tube, 19 mm long (31 setigers), 3.5 mm wide, same data as holotype.

Additional material. WESTERN AUSTRALIA - AM W20564: complete juvenile, 14 mm long (60 setigers), 1.5 mm wide, same data as types.

Complete specimens range from 14 mm in length (60 setigers), 1.5 mm in width to 45 mm in length (98 setigers), 3.5 mm wide.

Diagnosis. Antennal styles with brown specks; four pairs of modified parapodia with bidentate pseudocompound hooks with long appendages; limbate setae without proximal shelves; 10-15 transverse pectinate setae with 15-20 teeth at setiger 40.

Description. Animals whitish, with diffuse brown specks on prostomium and anterior part of

body. Brown rings on inner side of antennal ceratophores, styles with brown specks.

Prostomium (Fig. 29A) anteriorly rounded, with subulate to ovate frontal palps. Ceratophores with 8-9 proximal rings and a longer distal ring (Fig. 29B). Styles relatively short, tapering

slightly towards distal end, ending bluntly. Posterior antennae to setiger 12-15, anterior laterals to 7-11. Styles with 16-18 interrupted longitudinal rows of sensory buds. Buds slightly raised; pores of serous glands forming complete circles. Nuchal grooves forming crescents. Ten-

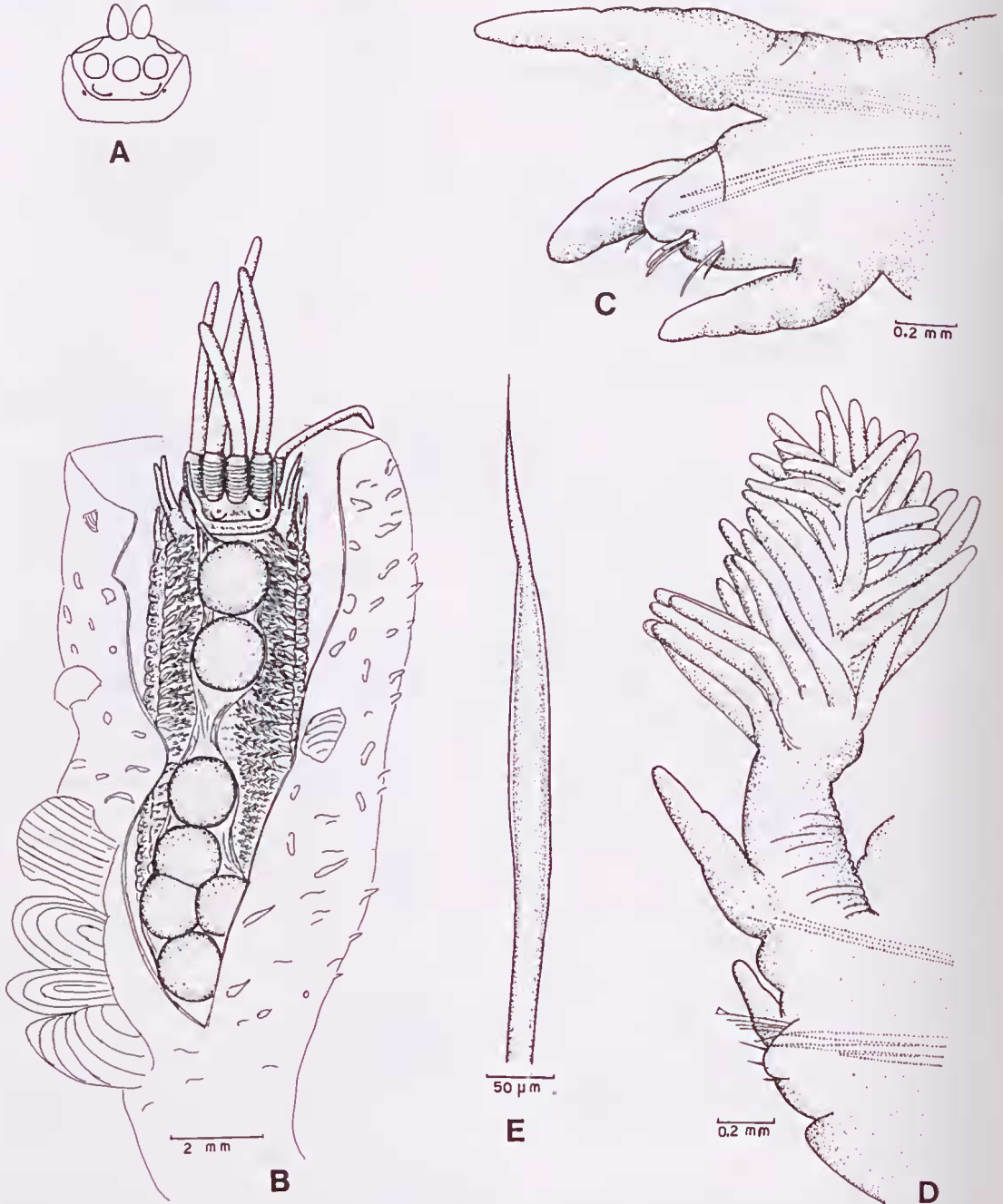


Fig. 29. *Diopatra gigova* sp. nov.: (B-D; holotype AM W19692; E; paratype AM W20563). A, stylized diagram of prostomium and peristomium, dorsal view; B, anterior end of worm with egg sac in opened up tube; C, parapodium 1, anterior view; D, parapodium 6, same view; E, median limbate seta from setiger 29.

tacular cirri about three times as long as peristomium (or equalling ceratophores); inserted distally on peristomium, almost lateral to posterior lateral antennae. Peristomium and following segments unusually short and compressed.

Anterior parapodia with rounded presetal lobe and subulate postsetal lobe (Fig. 29C). Presetal lobe present to setiger 6, postsetal lobe becoming gradually smaller but remaining as small boss to end of body. Dorsal cirri subulate, becoming more slender posteriorly; ventral cirri subulate on anterior 4 setigers. Spiralled branchiae (Fig. 29D) from setiger 5, first 10 pairs best developed with 5-6 whorls, reaching to peristomium (base of ceratophores) when extended anteriorly (or just touching middorsally). Individual filaments short and thick. Number of filaments decreasing gradually; 2-3 remaining at setiger 30, one at setiger 42, absent shortly thereafter.

Modified parapodia (setigers 1-4) with 1-2 slender upper limbate setae and bidentate pseudocompound hooks with moderately long appendages and pointed hoods. Each parapodium with 1 large median (Fig. 30A) and 2-3 less robust hooks projecting from main setal pocket, and 1-2 slender hooks (Fig. 30B) from small lower pocket.

Unmodified parapodia (setiger 5 onwards) with pectinate and limbate setae. Pectinate setae (Fig. 30C) with 13-20 teeth in transverse combs; 10-15 pectinate setae present per parapodium at setiger 30-40. Limbate setae hardly serrated, with narrow wings, some with swollen distal ends (Fig. 29E). Lower limbate setae replaced by 2 bidentate subacicular hooks from setiger 12-13.

Pygidium with two pairs of very short anal cirri.

Mandibles (Fig. 30D) with slender shafts and high, calcareous cutting plates each with one deep indentation. Most of shaft darkly sclerotized (black) except proximal part lacking sclerotization completely. Maxillae (Fig. 30E) weakly sclerotized, of light grey to brown colour with some black markings on carriers. Maxilla I strongly curved and slender. Mx II large plates with laterally protruding rami. Maxillary formula (based on 2 types): Mx I = 1 + 1; Mx II = 5 (6) + 7; Mx III = 6 + 0; Mx IV = 5 + 8 (7); Mx V = 1 + 1.

Tubes consisting of tough, parchment-like inner layer with an outer layer of muddy sand, pieces of vegetation and shells attached on angle as typical for genus.

Etymology. The name refers to the very large ova.

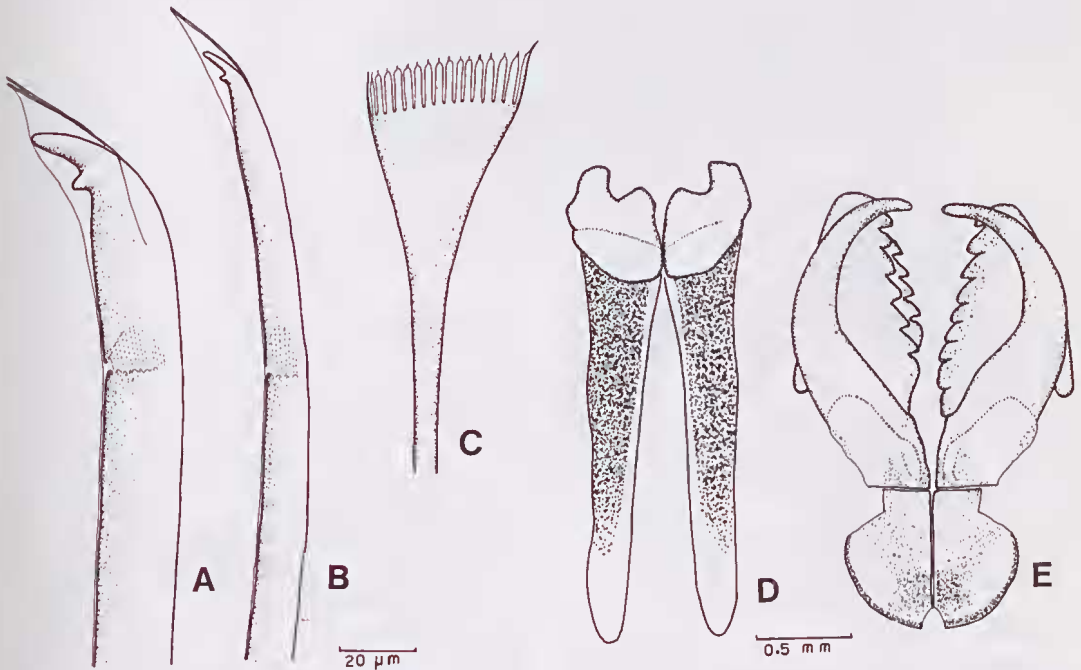


Fig. 30. *Diopatra gigova* sp. nov.: (A-C: holotype AM W 19692; D-E: paratype AM W 20563). A, large median pseudocompound hook from setiger 1; B, slender pseudocompound hook from same; C, pectinate seta from setiger 40; D, mandibles; E, maxillae (Mx IV and V omitted).

Remarks. The affinities of *D. gigova* have been discussed above (see remarks under *D. lilliputiana*).

Biology. As the holotype was extracted from its tube, it was found to cradle an egg sac with nine huge eggs on its dorsal surface between the branchiae from setiger 2-25 (Fig. 29B). The egg sac is a thin mucous bag, attached to the tube 1.5 cm from its distal end. The eggs are flattened, with a diameter of 1400 μm , and show no signs of development. The holotype is split ventrally between setigers 68 and 69 and this may possibly have been the exit for the eggs.

Distribution. *Diopatra gigova* is known only from the Dampier Archipelago, Western Australia (Fig. 6); intertidal.

***Diopatra aciculata* Knox and Cameron**
(Figs 6, 31-35)

Diopatra aciculata Knox and Cameron, 1971:31, figs. 20-25 (Port Phillip Bay, Melbourne, Victoria); Day and Hutchings 1979:118 (check-

list); Paxton 1986:19, 38, fig. 12 (juvenile colour patterns).

Type material. HOLOTYPE - NMV G1748: incomplete specimen, 45mm long (66 setigers), 4.5 mm wide, Port Phillip Survey, area 2(201), Hobson's Bay, Melbourne, Victoria, less than 6 m, 22 March 1963.

Additional material. NEW SOUTH WALES - AM W20407: 4, Sydney, Balmoral; AM W12280: 1; AM W13761: 1; AM W13764: 1; AM W20376: 1; AM W20378: 1, Sydney, Botany Bay; AM W3770: 2, Sydney, Camp Cove; AM W199451: 2, Sydney, Careel Bay; AM W20377: 4, Sydney, Chinaman's Beach; AM W6256: 29; AM W6257: 2; AM W6259: 30; AM W6266: 3. AM W6267: 3, Sydney, Long Bay. SOUTH AUSTRALIA - SAM E2154: 1; SAM E2155: 2, Adelaide, Barker's Inlet; AM W14114: 1, Adelaide, Outer Harbour; AM W6001: 7; AM W20404: 1; AM W20405: 4, Adelaide, St. Kilda; AM W20406: 2, Port Gawler; AM W6778: 2; SAM E2156: 8; SAM E2157: 1; SAM E2158: 3, Torrens Island. WESTERN AUSTRALIA - AM W5606: 20; AM W5640: 11; AM

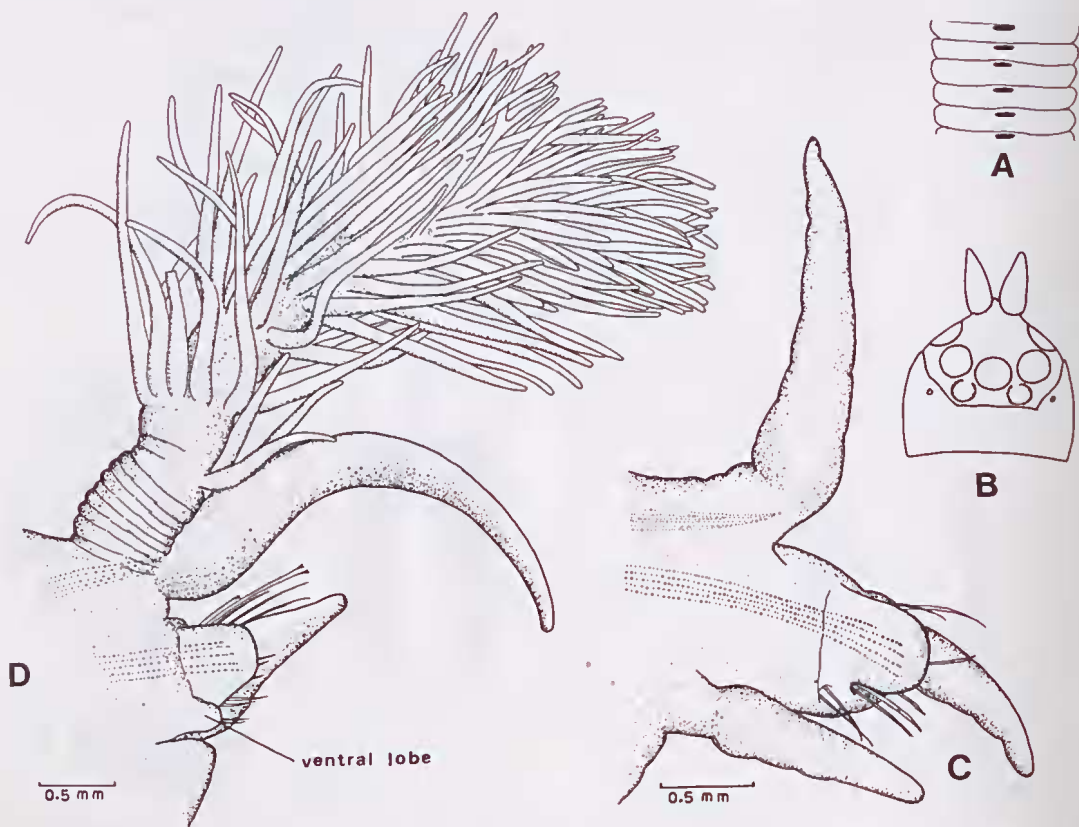


Fig. 31. *Diopatra aciculata*: (AM W6001). A, dorsal colour pattern of anterior segments; B, stylized diagram of prostomium and peristomium, dorsal view; C, parapodium I, anterior view; D, parapodium 6, same view.

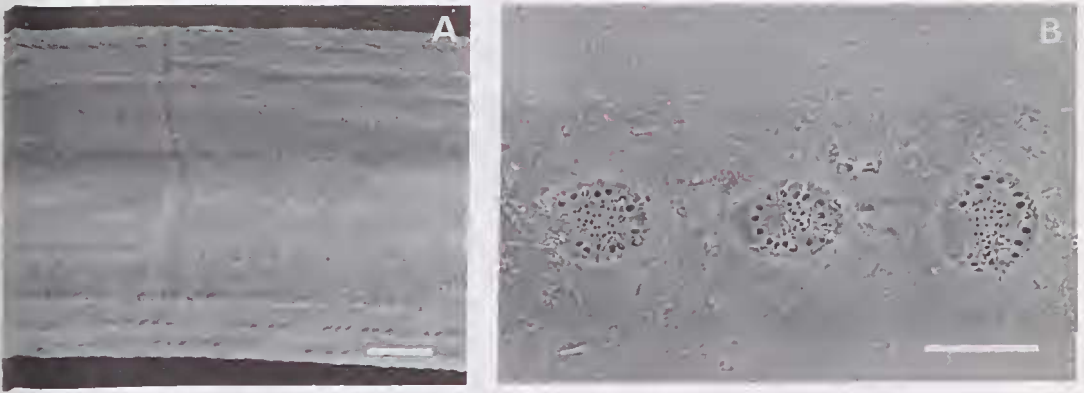


Fig. 32. Scanning electron micrographs of antenna of *Diopatra aciculata*: A, rows of sensory buds (scale 100 μ m); B, enlarged sensory buds (scale 10 μ m).

W6812: 4; AM W20408: 3, Bunbury, Fisherman's Jetty; AM W5605: 2; AM W5638: 11; AM W5639: 5; AM W5641: 19, Bunbury, Leschenault Estuary; WAM 31-79: 5; WAM 32-79: 2; WAM 33-79: 1; WAM 34-79: 1; WAM 36-79: 3; WAM 37-79: 2; WAM 42-79: 2; WAM 44-79: 1, Cockburn Sound; WAM 2-73: 3, Preston Point, Swan Estuary.

Complete specimens range from 11 mm in length (60 setigers), 0.7 mm in width to 340 mm in length (265 setigers), 9.0 mm in width. The greatest width of incomplete specimens is 11.5 mm.

Diagnosis. Ventral parapodial lobe on setigers 5-15; pectinate setae with 5-10 teeth; very long dorsal cirri; brown mid-dorsal bars.

Description. Anterior part of freshly preserved specimens often mottled brownish, fading quickly to very pale. Dark brown persistent pigment present as rings on inner side of ceratophores and as short transverse mid-dorsal bar on anterior margin of segment from about setiger 1-20 (Fig. 31A); more complex pattern of lines and patches in juveniles (see Paxton 1986, fig. 12).

Prostomium (Fig. 31B) anteriorly slightly extended and pointed, with a subulate frontal palp attached either side of apex. Ceratophores of antennae with 13-15 (10-17) proximal rings and a longer distal ring; ceratophores of posterior lateral antennae longest with 2-3 more rings than others. Styles short to moderately long, gradually tapering, ending in blunt tips; posterior antennae about equal to setiger 13 (8-15), anterior laterals to 3 (2-5). Styles with 20-22 interrupted longitudinal rows of sensory buds (Fig. 32A); buds flat, circles clearly demarcated, pores of serous glands irregularly spaced (Fig. 32B). Nuchal grooves in large specimens forming almost complete circles. Tentacular cirri about 3

(2-3) times as long as peristomium; inserted subdistally on long peristomium, almost lateral to posterior lateral antennae.

Anterior parapodia with rounded presetal, and long, subulate, postsetal lobes (Fig. 31C). Presetal and postsetal lobes becoming gradually smaller, presetal lobe disappearing by setiger 15-20, postsetal remaining as distinct conical lobe to end of body. Ventral lobe (Fig. 31D) present on setiger 5 to about 15-20; most distinct on setigers 6-11, then shifting more dorsally, forming new presetal lip by setiger 20-25. Dorsal cirri subulate, very long, attaining greatest length in branchial region, reaching up to mid-dorsum, thereafter gradually shortening, becoming very slender in posterior region. Ventral cirri subulate on ante-

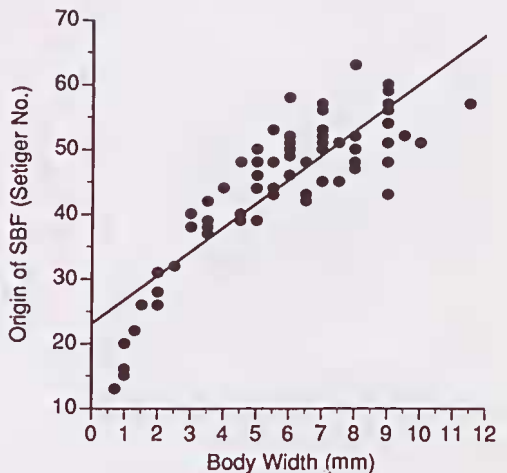


Fig. 33. *Diopatra aciculata*: Relationship between body width of specimens and origin of single branchial filaments (SBF) [$r^2 = 0.727$, $y = 3.7x + 23.1$, $P < 0.0001$ (significance of overall regression)].

rior 4 setigers. Spiralled branchiae from setiger 4 (4-5), best developed on setigers 7-20 with up to 20 whorls reaching to peristomium when extended anteriorly, distal whorls often close together, giving bushy or brush-like appearance.

Branchial filaments relatively long, proximally thick, tapering towards tips; decreasing gradually after setiger 20, single filaments from setiger 41 (10-60) depending on size of worm, absent shortly thereafter (Fig. 33).

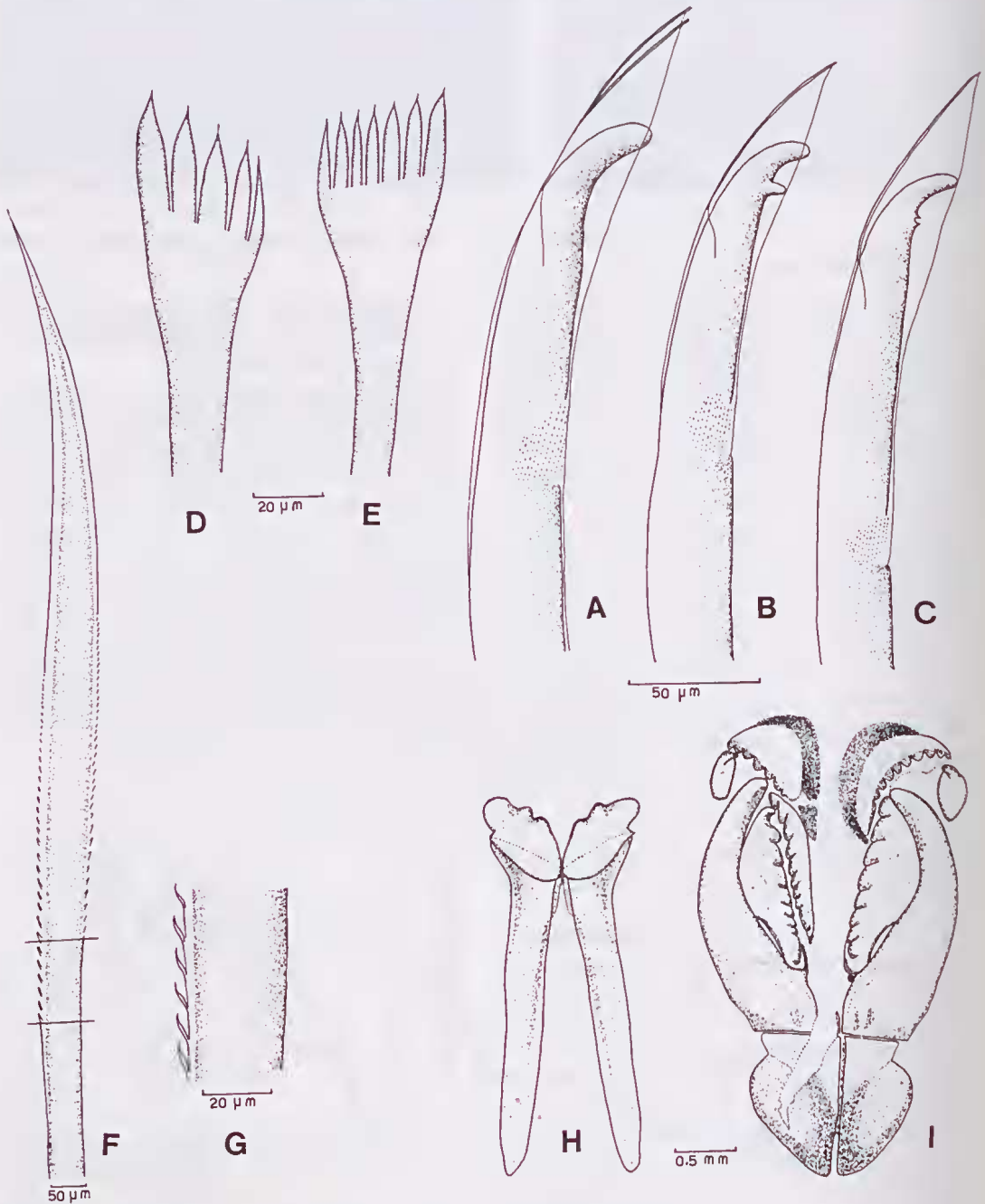


Fig. 34. *Diopatra aciculata*: (A-E: AM W6001; F-G: AM W20406; H-I: AM W20404). A, falcate pseudocompound hook from setiger 1; B, bidentate pseudocompound hook from same; C, weakly tridentate pseudocompound hook from same; D, pectinate seta from setiger 40; E, same from setiger 20; F, upper limbate seta from setiger 40; G, enlargement of same; H, mandibles; I, maxillae (tear in left carrier and Mx 1).

Modified parapodia (setigers 1-3 or 4) with 1-2 slender upper limbate setae and weakly pseudocompound hooks with moderately long appendages and long, pointed hoods. Each parapodium with 1 large median and 2-3 less robust hooks projecting from main setal pocket, and 2-3 slender hooks from small lower pocket. Tips falcate (Fig. 34A) and bidentate (Fig. 34B), occasionally weakly tridentate (Fig. 34C) where the small second and third teeth probably represent a deformed second tooth.

Unmodified parapodia (setiger 4 or 5 onwards) with pectinate and limbate setae. Pectinate setae with 5-10 teeth in transverse to slightly oblique combs (Fig. 34D, E); 10-15 pectinate setae present at setiger 40. Limbate setae coarsely serrated after setiger 35-45 (Fig. 34F, G). Lower limbate setae replaced by 2 bidentate subacicular hooks from setiger 14 (10-23) depending on size of worm (Fig. 35).

Pygidium with two pairs of short anal cirri; dorsal pair about as long as last 6 setigers, ventral pair one third thereof.

Jaws (Fig. 34H, I) of large specimens darkly sclerotized; almost black. Mandibles with slender shafts and high calcareous cutting plates with two weak indentations each. Maxillary formula (based on 10 specimens): Mx I = 1+1; Mx II = 6-9 + 5-10; Mx III = 5-8 + 0; Mx IV = 5-8 + 6-9; Mx V = 1+1.

Tube composed of whitish, tough, parchment-like inner lining, and outer covering of sand and minute pieces of shelly remains, giving it a smooth appearance, interrupted by occasional larger pieces of seaweeds or shells embedded towards the distal end.

Remarks. *Diopatra aciculata* is very similar to *D. neapolitana* Delle Chiaje, 1841. So much so, that other than slightly longer dorsal cirri and a smoother tube in the former, I could observe no distinct differences. Nevertheless, *D. aciculata* is retained as a separate species until more information to the contrary becomes available.

Knox and Cameron named the species for its conspicuous acicula. However, this is not a unique feature, but is also present in other large species of *Diopatra*. The authors described and figured (Knox & Cameron, 1971:31, Fig. 22) the secondary tooth of the bidentate hooks as "forming a rounded knob". This impression must be due to an optical illusion. Parapodium 3 of the holotype was examined and found to have bidentate and weakly tridentate hooks as figured here.

Biology. Specimens collected in November, January and March contained eggs (largest measuring 200-230 μm in diameter) or mature sperm. No eggs or developing young were found in any tubes or attached to them. The changes of the colour pattern from juvenile to adult were discussed and illustrated in Paxton (1986:19, fig. 12).

Distribution. New South Wales, Victoria, South Australia, Western Australia (Fig. 6); intertidal to 66 m.

DISCUSSION

Taxonomy. Species of *Diopatra* are superficially very similar. Their identification is frustrated by the lack of clear diagnostic features. Setae, which are generally such useful characters in specific polychaete classification, are too generalized in this genus to be of much help. In the present study a wide range of characters was examined to define the species by combinations of characters. These sets of characters may be different from species to species. A summary of all species treated here is given in Table 2.

Most species in the genus are relatively large. This presents a problem in that certain characters are size-dependent and vary with age. In the four common species, this aspect has been investigated for two characters: the extent of the branchial region (as indicated by the reduction of

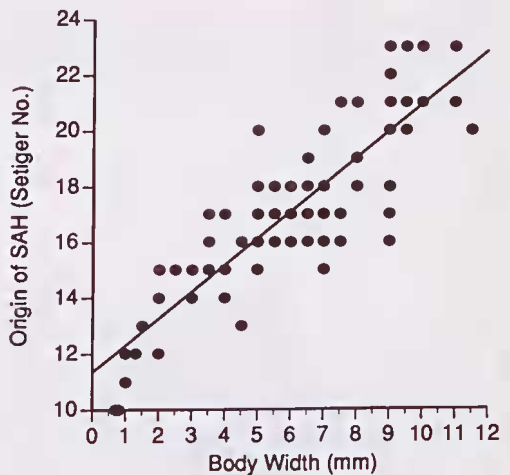


Fig. 35. *Diopatra aciculata*: Relationship between body width of specimens and origin of subacicular hooks (SAH) [$r^2 = 0.735$, $y = 0.96x + 11.3$, $P < 0.0001$ (significance of overall regression)].

Table 2. Comparison of Australian species of *Diopatra*.

	<i>D. amboinensis</i>	<i>D. dentata</i>	<i>D. maculata</i>	<i>D. oligopectinata</i>	<i>D. albinandibulata</i>
Max. length (mm)/ no. of setigers	170/320	245/355	170/240	45+/61+	73/145
Max. width (mm) at setiger 10	6.0	7.0	9.0	6.0	3.5
Colour pattern	overall brown to banded long	brown specks to overall brown short to moderately long	brown spots	brown specks	brown specks
Antennae	9-22	7-16	moderately long	moderately long	long
Ceratophores	brown rings	brown specks	brown spots	brown specks	brown specks
no. of rings	9-15	9-13	10-13	9-12	8-11
Styles	brown specks	brown band	brown band	brown specks	brown band
pigmentation	circle	circle	circle	semicircle	semicircle
sensory buds, shape	16-18	24-26	16-18	16-18	16-18
no. of rows	3/4 circle	3/4 circle	3/4 circle	3/4 circle	semicircle
Nuchal groove	very long	moderately long	moderately long	moderately long	moderately long
Tentacular cirri	long	up to set. 60 (Fig. 9)	long	moderately long	short
Branchiate region	up to set. 70 (Fig. 3)	absent	up to set. 68 (Fig. 14)	setiger 50-60	up to setiger 48
Ventral lobe on anterior parapodia	absent	pseudocompound	absent	absent	absent
Setae	short	pseudocompound	pseudocompound	pseudocompound	pseudocompound
appendage	bidentate	short to long	short	long to very long	bidentate
tip	transverse	bidentate	falcate to weakly bidentate	bidentate	bidentate
pectinate setae, shape	15-20	transverse	transverse	transverse	transverse
no. of teeth	10-20	11-20	15-22	6-11	18-24
no. of setae at set. 40	present	5-15	15-20	2-8	4-8
limbate setae, prox, shelf	present	present	present	present	present
subacicular hooks, origin	up to set. 23 (Fig. 4)	up to set. 18 (Fig. 11)	up to set. 18 (Fig. 16)	setiger 13-16	setiger 11-15
no. of indentations on calcareous plate	two	one	two	two	two
colour of shafts	black	black	dark brown oblique stripe from outer prox. to inner distal part	medially brown	white
Maxillae	MxI with medially extended falcate arch				
characteristic	none; L only; L & R	none; L only; L & R	L only	L only	L only; L & R
presence of MxIII	?	?	egg attached to tube	?	egg sac attached to tube
brood care	thousands	thousands	hundreds	?	250 in egg sac
number of eggs	200-230	240-260	350	?	300
diameter of eggs (μ m)	Ambon, W.A, NT, Qld.	NSW, SA	W.A, NT, Qld.	WA	Bowen, Qld.
Distribution (Fig. 6)					

Table 2. (cont.) : Comparison of Australian species of *Diopatra*.

	<i>D. lilliputiana</i>	<i>D. hanleyi</i>	<i>D. gigova</i>	<i>D. aciculata</i>
Max. length (mm)/ no. of setigers	31/125	65+/135+	45/98	340/265
Max. width (mm) at setiger 10	2.0	2.5	3.5	11.5
Colour pattern	brown specks	brown presetal lobes & bases of dorsal cirri	brown specks	brown middorsal bars on anterior setigers
Antennae				short to moderately long
relative length	short	short	short	8-15
posterior three to setiger	6-13	10-13	12-15	10-17
Ceratophores	brown specks	brown rings	brown on inner side	brown on inner side
no. of rings	5-8	7-9	8-9	10-17
Styles	brown band	brown specks	brown specks	brown specks
pigmentation	semicircle	?	circle	circle
sensory buds, shape	10-12	16-18	16-18	20-22
no. of rows	crescent	crescent	crescent	3/4 to almost circle
Nuchal groove	moderately long	moderately long	long	very long
Tentacular cirri	very short	moderately long	short	moderately long
Branchiate region	setiger 26-37	setiger 50-60	setiger 42	up to set 60 (Fig. 33)
Ventral lobe on anterior parapodia	absent	absent	absent	present
Setae	pseudocompound	pseudocompound & simple	pseudocompound	weakly pseudocompound
anterior hooks	short	moderately long	moderately long	moderately long
appendage	bidentate & falcate	bidentate	bidentate	bidentate & falcate
tip	slightly oblique	transverse	transverse	transverse to slightly oblique
pectinate setae, shape	25-30	20-25	13-20	5-10
no. of teeth	3-5	3-14	10-15	10-15
no. of setae at set. 40	absent	absent	absent	absent
limbate setae, prox. shelf	setiger 10-14	setiger 16-18	setiger 12-13	up to set. 23 (Fig. 35)
subacicular hooks, origin	one	two	one	two
no. of indentations on calcareous plate	laterally brown	dark brown	black, except proximal part	black
colour of shafts	MxI with medially extended	MxI with medially extended	MxII with laterally protruding ramus	
characteristic	falcate arch	falcate arch	ramus	
Maxillae	L only	L only	L only	L only
presence of NxIII	brooding in tube	?	brooding in tube	?
Biology	40 in egg sac	thousands	9 in egg sac	thousands
number of eggs	400-700	170-180	1,400	200-230
diameter of eggs (µm)	W/A	Darwin, NT	Dampier Arch., WA	NSW, Vic, SA, WA
Distribution (Fig. 6)				

branchiae to a single filament) and the first occurrence of subacicular hooks. For each of these characters the first occurrence or origin (expressed as setiger number) is plotted against the width of the worm as a measure of size. The two characteristics are size-dependent for all four species. With respect to the first occurrence of single branchial filaments, all four species show a similar pattern (Figs 3, 9, 14, 33).

While there is also a clear relationship between size and the first occurrence of subacicular hooks in *D. amboinensis* (Fig. 4), *D. maculata* (Fig. 16) and *D. aciculata* (Fig. 35), this relationship is not so marked for *D. dentata* (Fig. 11) as can be seen by the slope of the regression (Fig. 11) for this species.

Species complexes. An analysis of the relationships must await a complete revision of the genus since it is obvious that the Australian species do not constitute a distinct group. However, it is possible to identify one, and perhaps two groups of species.

Five species share a number of character states and are here considered as the *D. amboinensis* complex. It includes *D. amboinensis*, *D. dentata*, *D. maculata*, *D. oligopectinata* and *D. albinandibulata*. All possess four pairs of modified parapodia, transverse pectinate setae with thick stems, and limbate setae with proximally serrated shelves. Symmetrical maxillae, i.e. the presence of both left and right maxilla III, were observed in three of the five species. This condition was found quite often in *D. amboinensis* and *D. dentata*, whereas it was never seen in other species (e.g. *D. aciculata*), even though greater numbers were examined. This seems to indicate that the condition is not due to *de novo* mutations, but is fixed in the gene pool, thus making its presence an indicator of relationships.

Of the remaining four species, *D. aciculata* definitely stands on its own. It is closer to the European *D. neapolitana* than to any of the Australian species.

Diopatra lilliputiana, *D. hanleyi*, and *D. gigova* have slender, weakly serrated limbate setae and pectinate setae with thin stems. In the first two species the maxilla III originates proximally almost at the level of the maxilla II, a characteristic that is not found in any of the other species. At the present time it can only be stated that these three species are not members of the *D. amboinensis* complex, and any statements about their degree of relationship would be mere speculation.

Reproduction and development. The general reproductive biology of onuphids has been reviewed by Paxton (1986) and Hsieh and Simon (1987). From previous reports we know that *Diopatra* eggs are relatively large, and development is either by lecithotrophic pelagic larvae or direct with brood care in the parental tube. The present paper reports new information on eight Australian species and attempts to relate the adult size, egg size, brood size and larval type to identify developmental patterns with respect to the method of spawning and brood care. All other available information is summarized and included, although the identity of the reported species is in some cases uncertain. Four developmental patterns are identified and discussed below; the species making up the various groups and their characteristics are listed in Table 3.

I. Brooding in parental tube - direct development. Six species brood their eggs in the parental tube. The adults are relatively small (up to 3.5 mm width), the eggs are large (600-1,400 μm) and few (8-50). Most of these reports are based on circumstantial evidence, i.e. eggs or larvae found in newly collected or preserved tubes. *Diopatra variabilis* Southern, 1921, has been studied in detail (Krishnan 1936). The young undergo direct development in the parental tube and leave the tube when they consist of more than 25 setigers. In some species the juvenile worms, upon leaving the parental tube, attach their own tubes to the parental one. Lieber (1931) reported that tubes of *Diopatra* n. sp. from Sumatra provided evidence that three generations of worms had built tree-like colonies of tubes.

II. Direct development in cocoon. Day (1960) reported that among empty *Diopatra* tubes dredged from False Bay, South Africa, he found a mud cocoon containing six post-larval *Diopatra* specimens of 8-15 mm. He stated that the juveniles had tentacular cirri and obvious spiral gills. It seems unlikely that they reached this stage of development by lecithotrophic nutrition, yet there would be no other source of food available in a cocoon. Therefore, this mode of development is doubtful, since the presumed cocoon may have been the remains of a broken tube.

III. Egg masses attached to parental tube - direct development. The adults are small to large (3.5 to 10.0 mm in width), the eggs are moderately large (280-350 μm) and in moderate to large numbers. The distal part of a tube of *Diopatra maculata* was covered by thousands of 3 to 4-setiger larvae in a jelly matrix. Although

Table 3. Summary of developmental characteristics in the genus *Diopatra*. I. Brooding in parental tube, direct development in cocoon; II. direct development in tube, direct development in cocoon; III. egg mass attached to parental tube, direct development; IV, broadcast spawning, free-swimming stage; ?, unknown.

Species	Locality	Max. width of adult (mm)	Max. egg diameter (µm)	Max. number of eggs	Observation	Reference Pattern	Developmental
<i>D. ?brevicirris</i> Grube, 1856 as <i>D. cuprea</i> Bosc, 1802	Madeira	?	?	?	11-setiger larvae in tube	Monro 1924	I
<i>D. ?sp. nov.</i> as <i>D. amboinensis</i> Aud. & M. Edw., 1833 as Java	Indonesia	3.0	?	?	up to 6-setiger larvae in tube	Lieber 1931	I
<i>D. ?sp. nov.</i> as <i>D. nova species</i> (sic)	Indonesia as Sumatra	?	"gigantic"	?	larvae in tube	Lieber 1931	I
<i>D. variabilis</i> Southern, 1921	India	3.0	600	30-50	eggs and larvae of various stages in tube; reared to 15-setiger stage in laboratory	Krishnan 1936	I
<i>D. liliputiana</i> , sp. nov.	W. Australia	1.3	700	40	up to 15-setiger larvae in tube	present study	I
<i>D. gigova</i> , sp. nov.	W. Australia	3.5	1400	8	eggs in tube	present study	I
<i>D. sp.</i>	S. Africa	?	?	?	6 juveniles (8-15 mm long) in mud cocoon	Day 1960	II
<i>D. maculata</i> , sp. nov.	W. Australia	9.0	350	1000's	3 to 4-setiger larvae in gelatinous matrix on outside of distal end of tube	present study	III
<i>D. albindibulata</i> , sp. nov.	E. Australia	3.5	280	250	3-setiger larvae in gelatinous egg sac attached to inside of distal end of tube	present study	III
<i>D. neapolitana</i> d. Chaije, 1841	Italy	10.0	?	?	eggs in gelatinous mass on distal end of tube	Lo Bianco 1898	III
<i>D. cuprea</i>	NE. U.S.A.	10.0	220	?	eggs released in jelly mass which readily dissolves in seawater; reared for 21 days in laboratory	Allen 1959	IV
<i>D. ?sugokai</i> Izuka, 1907 as <i>D. neapolitana</i>	Japan	10.0	200	?	artificial fertilization; reared in laboratory	Choe 1960	IV
<i>D. ?sp. nov.</i> as <i>D. cuprea</i>	SE. U.S.A.	2.0	200	3200	? eggs in body cavity	Fauchald 1983	?
<i>D. ornata</i> Moore, 1911	SW. U.S.A.	3.0	235	900	? eggs in body cavity	Fauchald 1983	?
<i>D. dextignatha</i> Paxton & Bailey-B., 1987	Hawaii, U.S.A.	1.8	180	?	eggs in body cavity	Paxton & Bailey-Brook 1987	?
<i>D. amboinensis</i>	N. Australia	6.0	230	1000's	eggs in body cavity	present study	?
<i>D. aciculata</i>	S. Australia	11.5	230	1000's	eggs in body cavity	present study	?
<i>D. dentata</i> Kinberg, 1865	E. Australia	7.0	260	1000's	eggs in body cavity	present study	?
<i>D. hanleyi</i> , sp. nov.	N. Australia	3.0	170	1000's	eggs in body cavity	present study	?

their subsequent developmental history is unknown, it seems reasonable to assume that they remain there until they start to build their own tubes which, in *D. cuprea* Bose, 1802, occurs as early as the 4-5 setiger stage (Allen 1959). Another Australian species, *D. albimandibulata*, attaches its eggs in a small bundle of about 250 eggs to the distal part of the tube.

In the Mediterranean, *D. neapolitana* has long been known to attach its many yellow eggs to the top of the parental tube in a brown, irregular, gelatinous mass of about one square centimetre in size (LoBianco 1898). Although the size and number of eggs per spawning and their fate appear to be unknown, it is assumed that they also undergo direct development.

IV. Broadcast spawning - free-swimming stage. The eggs of *D. cuprea* are relatively small (220 μm) and are released in a jelly mass that readily dissolves in seawater (Allen 1959), indicating broadcast spawning. The development of *D. cuprea* has been studied in detail by Allen (1959). The larvae were free-swimming by 24 hours and settled to the bottom after four days. The literature reports of *D. cuprea* egg masses on Woods Hole beaches have been confused with those of *Americanuphis magna* (Andrews, 1891) (see Allen 1959). Fauchald (1983) calculated the number of eggs of a single spawning for a species from Florida that he reported as *D. cuprea*. However, these specimens and their eggs were much smaller than *D. cuprea* from Massachusetts; they probably represent a new species. A species from Japan, probably *D. sugokai* Izuka, 1907, reported as *D. neapolitana*, was studied by Choe (1960). The artificially fertilized eggs developed into free-swimming larvae and settled to the bottom after about three days.

The developmental pattern for the last seven species listed in Table 3 is unknown. However, they all have relatively small eggs, ranging from 170-260 μm . Considering the observed developmental patterns it seems unlikely that they brood in the tube. Careful examination of the tubes of some common species such as *D. amboinensis*, *D. dentata* and *D. aciculata* has revealed no signs of eggs associated with the tubes. It is, therefore, assumed that these three species are free spawning.

A better understanding of the reproductive patterns provides additional characters to help solve the taxonomic problems of this interesting genus. This will be of particular importance for the taxonomically difficult *D. cuprea* and *D. neapolitana* complexes, as has been demonstrated here.

ACKNOWLEDGEMENTS

I am grateful to the following individuals for providing research space and hospitality at their institutions and/or the loan of material: Pat Hutchings (AM); J. Renaud-Mornant, M.N. Helléouet and J.-L. Justine (MNHN); Suzanne Boyd (NMV); Roy Oleröd (NRS), Russell Hanley (NTM); Patricia Mather (QM); Shane Parker (SAM); Loiset Marsh (WAM) and Gesa Hartmann-Schröder (ZMH). Special thanks go to Charlotte Watson-Russell (NTM) for seaba collections in the Sydney area. Many thanks to Suzanne F. Doyle and Jenny Norman (MU) for the scanning electron micrographs and photography, and to Barbara Duekworth, Rees Griffiths and Mandy Reid (MU) for help with graphs. I also thank the two anonymous reviewers for their helpful comments.

The work was supported by Macquarie University Research Grants and by an Australian Biological Resources Study Grant. This is publication number 111 of the Research Unit for Biodiversity and Bioresources, Macquarie University.

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Accepted 10 December 1991